THE EVOLUTION OF DEVELOPMENTAL STRATEGY IN CRETACEOUS SPATANGOID SEA URCHINS

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by John Alexander Cunningham.

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ABSTRACT

Sea urchins, like many marine invertebrates, have two major strategies for larval development. Some species have planktotrophic (feeding) larvae, which feed in the water column for a period of weeks to months prior to metamorphosis into a juvenile sea urchin. Other species have non-planktotrophic (non-feeding) larvae, which are produced in much smaller numbers and do not feed but are instead supplied with nourishment in the form of an egg for the much shorter period they spend prior to metamorphosis. This thesis aims to understand the evolution of these larval modes by focusing on the Cretaceous spatangoid echinoids, where larval mode can be inferred from adult tests, which have an abundant fossil record.

The taxonomy of the group was revised in order to ensure that species used in the subsequent analyses are biologically meaningful. Phylogenetic analyses of the species considered valid were then undertaken to provide hypotheses of evolutionary relationships that form the basis of analyses of the evolution of larval strategy. Larval modes were determined for a large number of species. When these data were mapped onto spatangoid phylogeny, non-planktotrophy was shown to have evolved independently on five occasions. The first occurrence of each of the five non-planktotrophic clades is in either the Campanian or Maastrichtian (the final two Cretaceous stages) with no instances of non-planktotrophy prior to the Campanian. There is no support for the hypothesis that non-planktotrophic groups originate preferentially at high latitudes, despite the fact that non-planktotrophic species are unusually abundant at these latitudes today. Analysis of raw data showed that there is a significant association between non-planktotrophic larval development and both increased speciation rates and reduced species longevity. However, when phylogeny was considered, it was not possible to discount the possibility that significant associations result simply from shared ancestry. No significant associations were identified between larval mode and geographical range, latitude or depth.

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1. INTRODUCTION

Many marine invertebrates have a two-phase life cycle with adults living on the sea floor and larvae in the water column. Each of these species employs one of two developmental strategies, termed planktotrophy and non-planktotrophy. Planktotrophic (feeding) larvae live and feed in the water column for a period of weeks to months before settling to the sea floor and metamorphosing into the juvenile. Non-planktotrophic (non-feeding) larvae are unable to feed and are instead nourished by an egg yolk for the hours to days that they spend in the water column (or brood pouch) prior to their metamorphosis.

The two strategies are of interest to developmental biologists, ecologists and evolutionary biologists and they are thought to be linked to factors such as geographical range, speciation and extinction rates and species longevity. But despite this wide interest in the evolution of developmental strategies, very little is known about the evolutionary history of developmental modes, or the factors that drive changes in mode. There are a number of important unanswered questions. Which developmental mode arose first? Are switches in mode scattered through time or concentrated in particular time intervals? Do they correlate with specific environmental conditions?

Palaeontological studies are important as they have the potential to answer these questions by adding the dimension of time, which is otherwise unavailable to biologists. Unfortunately the poor fossil record of developmental stages and our limited knowledge of evolutionary relationships have hitherto hampered such studies. However, fossil sea urchins offer a unique opportunity to address these questions because it is possible to determine the developmental strategy from an inspection of the adult skeleton and because their complex morphology provides abundant

characters, making it relatively straightforward to resolve evolutionary relationships.

This study focuses on the Cretaceous spatangoid sea urchins, which represent an ideal study group because they are common fossils and lived in a wide range of environments and palaeolatitudes, meaning that the relationships between these factors and developmental strategy can be explored. The group includes both feeding and non-feeding species and it spans the time period when non-feeding larvae were thought to have first evolved within echinoids.

Here I revise the taxonomy of the group and use cladistic methodology to produce hypotheses of evolutionary relationships between the species. Data on developmental strategies of the species are then plotted on to the resulting evolutionary trees in order to determine which type of larvae was present in the first members of the group, and how many switches in developmental mode have occurred. The latitudes and longitudes, the environments and the time periods in which each species lived are gleaned from the literature; standard statistical techniques are then used to assess whether any of these factors correlate with developmental mode.

1.1. EVOLUTION AND DEVELOPMENT

1.1.1. The 'evo-devo' revolution

The study of the evolution of larval strategies integrates evolutionary and developmental biology. Evolution is the change in the heritable traits of a population over successive generations, while development involves the transformation of an individual from an egg to an adult. Thus, both evolution and development involve the variation of morphology through time and it was

first recognized in the nineteenth century that the two processes must be intimately linked (e.g. von Baer 1828; Haekel 1866).

However, for much of the twentieth century the disciplines of evolutionary biology and developmental biology have been disconnected from one another. The Modern Synthesis (e.g. Dobzhansky 1937; Huxley 1942; Mayr 1942; Simpson 1944) of the 1930s and 1940s, which produced the integration of Darwin's (1859) theory of evolution by natural selection and Mendel's (1866) theory of inheritance and forms the foundations of modern evolutionary biology, almost completely excluded the process of development. The Synthesis thus treated embryology as a 'black box' that somehow transformed genetic information into functional animals (Carroll 2005). Developmental studies, meanwhile, were largely focused on experimental embryology – the manipulation of embryos in order to understand the forces that drive their development. These studies tended to concentrate on a small number of well understood 'model organisms', rather than considering an evolutionary framework.

The past twenty to thirty years has seen the revolutionary reintegration of the two disciplines and the birth of the new science of evolutionary developmental biology (often referred to as "evo-devo"). This reconciliation came about largely because of the invention of new techniques in developmental biology. In particular, advances in gene cloning techniques allowed developmental geneticists not only to identify the genes responsible for body patterning in the fruit fly *Drosophila* (Lewis 1978; Wakimoto & Kaufman 1981; Scott & Weiner 1984; McGinnis *et al.* 1984b), but also to make the highly unexpected discovery that these same genes were present in distantly related animals (McGinnis *et al.* 1984a). This was followed by the even more surprising discovery that these genes were employed for the same developmental function across the animal kingdom. For example, the *Drosophila* gene *eyeless*, which is essential for eye formation, was found to

be homologous to the genes *Small eye* and *Aniridia* that are responsible for eye formation in mice and humans respectively (Quiring *et al.* 1994).

These discoveries overturned the widely held assumption that the different animal groups would have unique genetic toolkits as a result of their unique functional requirements. Furthermore, the similarity in genetic toolkits between phyla provided developmental data containing a strong evolutionary signal, thus making developmental processes relevant to the study of evolutionary mechanisms and events in evolutionary history (Raff 1996, 2000). This re-established the importance of understanding the interplay between evolutionary and developmental processes.

1.2. THE EVOLUTION OF DEVELOPMENTAL STRATEGY

1.2.1. What is developmental strategy?

Understanding the evolutionary history of development and the relationship between development and evolutionary events occurring in Deep Time are major goals of evolutionary developmental biology. An important part of this is to unravel the evolutionary history of the larval strategies used by animals to disperse and to develop into adults.

Marine invertebrates often have a two-phase life cycle in which the adults live on the sea floor while the larvae live in the water column. The adults are relatively slow moving with narrow environmental tolerances, so the larval stage offers them their main opportunity for dispersal. Each species employs one of two developmental strategies for dispersal, namely planktotrophy and non-planktotrophy. Planktotrophic (feeding) larvae live and feed in the water column for a period of weeks to months before settling to the sea floor and metamorphosing into the juvenile sea urchin. Non-planktotrophic (non-feeding) larvae are unable to feed and are instead

nourished by an egg for the hours to days they spend prior to their metamorphosis. Non-planktotrophs can be subdivided into those that are brooded by the female, and those that inhabit the water column, which are termed planktonic non-planktotrophs (see Table 1.1 for summary of terminology).

The switches between one strategy and the other are of interest to developmental biologists who have found that they involve large changes in early development with little change in the adult. For example, two closely related species in the camaradont echinoid genus *Heliocidaris* have radically different larvae and yet virtually indistinguishable adults (e.g. Raff 1996, chapter 7). This is a surprising finding as it had been thought that such major developmental changes would have fatal effects later in development.

Ecologists and evolutionary biologists are also interested in the shifts in developmental mode, as it is thought that developmental modes are linked to a number of macroevolutionary and palaeobiogeographical factors (for review see Jablonski & Lutz 1983), and these may have important implications for conservation biology (e.g. Cowen *et al.* 2006). Firstly, developmental strategy is thought to be linked to the geographical range of a species: non-planktotrophs spend less time in the water column, so they are thought to disperse less far and, as a result, to have narrower geographical ranges. As a result of their narrower ranges non-planktotrophs are thought to be more likely to be wiped out by a local catastrophe, leading to higher extinction rates and reduced species longevities. In addition, non-planktotrophic species are expected to have greater speciation rates because their lower dispersal means that it is easy for a population to become genetically isolated. It has also been suggested that larval mode may correlate with latitude (e.g. Thorson 1950), temperature (e.g. Foster 1974) and depth (e.g. Thorson 1950). However, despite much discussion of these ideas in the literature, there have hitherto been remarkably few tests of

them. This is particularly true for those factors that can only be studied using fossil data.

<table>
<tr><th></th><th>Thorson (1950); Ockelmann (1965)</th><th>Scheltema (1978); Crisp (1974)</th><th>Shuto (1974); Strathmann (1978)</th><th>Jablonski & Lutz (1980, 1983)</th><th colspan="2">Jeffery & Emlet (2003)</th><th colspan="2">This thesis</th></tr>
<tr><td>Free-swimming, feeding larvae</td><td>Planktotrophic</td><td rowspan="2">Pelagic</td><td>Planktotrophic</td><td>Planktotrophic</td><td colspan="2">Planktotrophic</td><td colspan="2">Planktotrophic</td></tr>
<tr><td>Free-swimming, non-feeding larvae</td><td>Lecithotrophic</td><td rowspan="2">Lecithotrophic</td><td rowspan="2">Non-planktotrophic</td><td rowspan="2">Non-planktotrophic</td><td>Lecithotrophic</td><td rowspan="2">Non-planktotrophic</td><td>Planktonic</td></tr>
<tr><td>Offspring emerge as benthic juveniles</td><td>Direct Development</td><td>Non-pelagic</td><td>Brooded</td><td>Brooded</td></tr>
</table>

Table 1.1: Table showing the various terms applied to larval strategy in the literature, and those used in this thesis. Because the term 'lecithotrophic' has been used in different ways in the literature, I prefer the term 'non-planktotrophic', which may be subdivided into planktonic and brooded non-planktotrophic strategies. Modified after Jablonski & Lutz (1983).

1.2.2 How can we study developmental strategy in fossil taxa?

Studies of larval mode in ancient taxa have, historically, involved comparative analysis of living representatives of lineages as a means of inferring the strategy of their last common ancestor. But, as Strathmann (1993) has noted, when comparisons are made between more distantly related taxa the reliability of the inferences diminishes.

The fossil record has the potential to yield important information on the evolutionary history of development, but the role of palaeontological data has, thus far, been limited. This is due in large part to the poor fossil record of developmental stages: while there are examples of fossilized larvae (e.g. Müller & Walossek 1986) and embryos (see Donoghue & Dong 2005 for review) it seems that their fossil record is strongly restricted, both temporally and taxonomically (Donoghue *et al.* 2006a). Furthermore, there may be biases against the preservation of directly developing embryos and non-cuticular primary larvae because of their size and fragility (Bengtson & Yue 1997; Donoghue *et al.* 2006a; Raff *et al.* 2006; Gostling *et al.*, 2008). The problem is compounded by the fact that the phylogenetic position of these fossils is often poorly constrained.

Fortunately, however, it has also been possible to infer developmental strategy from fossilized adults of some taxa that are commonly preserved in the geological record. The first taxon in which this was realized was the molluscs. Here the larval shell forms the first part of the adult shell called the protoconch, which is then added-to sequentially but never lost. Thus, scanning electron microscopy of well-preserved adult shells allows us to examine the shape and size of the larval shell. This information allows the inference of developmental strategy because non-planktotrophs have larger yolky eggs and this difference is reflected in the size and shape of the

protoconch (see Jablonski & Lutz (1983) for a detailed discussion of the methodology). This technique has been applied in the following studies:

- Hansen (1978) studied volutid gastropods from the Paleogene of the Gulf Coast. 'Planktonic' larvae were found to have a mean species duration that was double that of "non-planktonic" larvae (4.4 m.y. vs 2.2 m.y.). In a later study Hansen (1980) found that the geographical ranges of planktonic species were also approximately double those of non-planktonic species.

- Jablonski (1982) found similar results in gastropods from the Late Cretaceous of the Gulf and Atlantic coastal plain: here planktotrophs were found to have a mean geographical range of 1500 km and a mean species duration of 6 m.y., whereas non-planktotrophic species had a mean geographical range of 610 km and mean species duration of 3 m.y.

- Nützel *et al.* (2006) found that planktotrophy first occurred in molluscs around the Cambrian-Ordovician boundary, thus corroborating findings from molecular clock studies (see section 1.2.3).

A similar methodology can be applied to brachiopods, where the presence of a larval mantle, and hence of a planktotrophic larva, can be determined from the morphology of the adult shell (see Freeman & Lundelius 1999, 2005 for detailed discussion of the methodology).

- Freeman & Lundelius (1999, 2005) found the opposite pattern to that identified by Nützel *et al.* (2006) for molluscs: namely planktotrophy being the only strategy in the early Palaeozoic with non-planktotrophy evolving in the Late Cambrian or Early Ordovician.

One weakness of these studies is that fossil molluscs and brachiopods tend to be relatively poor in characters that are suitable to be used in phylogenetic analysis, meaning that their evolutionary relationships are rarely well known. As a result, the authors of the studies described above were unable to constrain the number of switches in larval mode, or to assess whether their findings were biased by the phylogenetic relationships of the group under study.

The other major group in which developmental strategy can be inferred from adult skeletons is the echinoids. Here, this can be achieved by using either morphological or crystallographic criteria. There are two morphological criteria that can be indicative of non-planktotrophic larvae, both of which rely on sexual dimorphism of the test. Firstly, some brooding non-planktotrophic species can be recognized by the presence of depressed areas on the test, called marsupia, where the larvae are sheltered during development (e.g. Philip & Foster 1971). Secondly, extreme sexual dimorphism in gonopore size can be used to infer non-feeding larval development (Emlet 1989); this is because the females may develop very large gonopores in order to accommodate the large yolky eggs of non-feeding larvae. Larval mode can also be inferred from the orientation of the crystallographic axes of the plates in the apical system (Emlet 1985, 1989). This is possible because the planktotrophic larva has skeletal calcite rods, the main function of which is to support the larval arms that are used in feeding; during metamorphosis some of the apical plates grow from the proximal ends of the rods – this imparts a characteristic crystallographic orientation to the plates. In non-planktotrophic larvae these rods are absent and the apical plates all form *de novo* at metamorphosis, producing a distinct pattern of c-axis orientations. The c-axis orientations are determined by growing calcite in optical continuity with that of the apical system plates (Okazaki *et al.* 1981) and then measuring the face poles using an optical goniometer; this methodology is

discussed in more detail in section 4.2. To date this technique has been used in only four studies:

- Emlet (1995) studied the relationship between developmental mode and species range in 215 Recent regular sea urchins. He found that species with pelagic, feeding larvae have significantly larger ranges than those with pelagic, nonfeeding larvae, but there is no difference in ranges between species with pelagic, nonfeeding larvae and those with brooded development.

- Jeffery & Emlet (2003) studied development in fossil temnopleurids from the Tertiary of Australia showing that planktotrophy was plesiomorphic for the clade and that non-planktotrophy evolved independently at least three times. They found the switches to be unidirectional with no reversals from non-planktotrophy to planktotrophy but they found no evidence of an ordered transformation from planktotrophy to planktonic non-planktotrophy to brooded non-planktotrophy. They also found that non-planktotrophs had significantly shorter species longevities, more restricted geographical ranges and higher speciation rates than planktotrophic taxa, but were unable to confirm that the stratigraphic and geographical patterns were unbiased by the phylogenetic relationships of the taxa.

- Jeffery *et al.* (2003) used a molecular phylogeny of Recent temnopleurids to study the evolution of developmental strategy; they found that a single switch from planktotrophy could account for all non-planktotrophic members of the clade.

- Jeffery (1997) carried out a broad overview of developmental strategy in all major echinoid clades, concluding that non-planktotrophy first

evolved immediately prior to the Cretaceous-Tertiary boundary and that it was adopted independently in five orders at this time. In spite of this study, the temporal distribution of developmental strategies within orders and at lower taxonomic levels remain poorly known. The present thesis aims to address this by studying one order, the spatangoids, in detail.

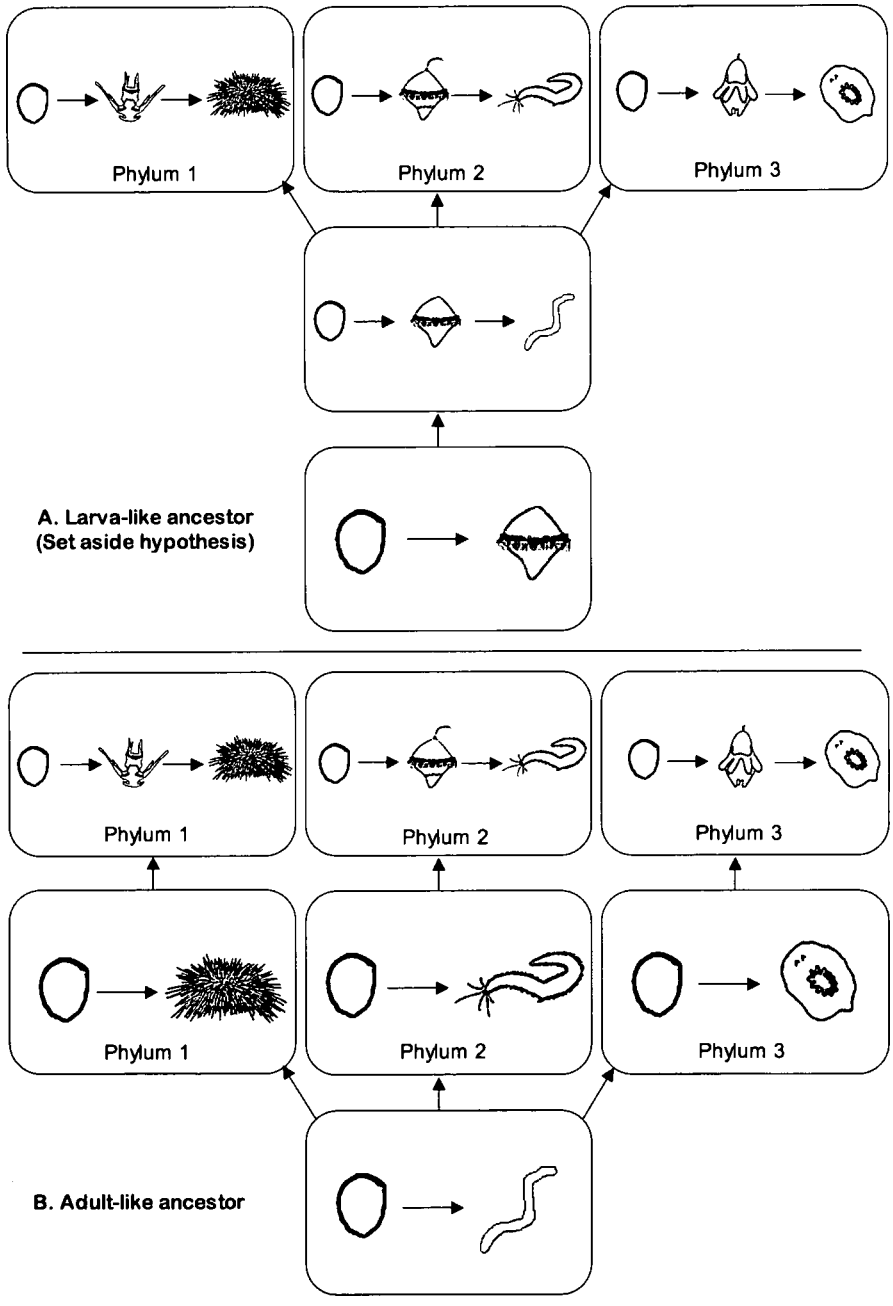

Figure 1.1: The competing hypotheses regarding the developmental strategy of the last common ancestor of bilaterians. (**A**) Larva-like ancestor. In this hypothesis each phylum evolves from a planktotrophic larva-like ancestor and independently evolves an adult body plan. This occurs via the evolution of cells termed set-aside cells, which form a rudiment that gives rise to the adult life phase at metamorphosis. (**B**) Adult-like ancestor. Here the adult body plan is primitive and the larval stage evolves convergently in each phylum by intercalation of larval features into its ontogeny. In this scheme set-aside cells evolve convergently allowing for rapid metamorphosis. Some images from Sly *et al.* (2003).

1.2.3. Which strategy is primitive for bilaterians?

This thesis examines the late Mesozoic evolution of non-planktotrophy from planktotrophy in spatangoid sea urchins. However, the question of whether planktotrophic development is primitive among the bilaterians (animals with bilateral symmetry) has provoked much controversy, and provides important context for the work in this thesis (see also Appendix 1 for a discussion of the plesiomorphic condition in echinoids). At stake is our interpretation of the early history of animals: if planktotrophic larval development is primitive it means larval characters are important for understanding high-level metazoan phylogeny and implies that development played an important role in the Cambrian 'explosion' (Conway Morris 1998; Sly *et al.* 2003). The competing hypotheses are outlined below and illustrated schematically in Figure 1.1.

Many traditional hypotheses argue that planktotrophy is primitive with direct development appearing later (Haekel 1874; Jägersten 1972; Davidson *et al.* 1995; Nielsen 2001). This is because: (1) most clades of directly developing taxa appear to be derived from planktotrophic ancestors (Strathmann 1978; Jeffery *et al.* 2003; Sly *et al.* 2003); (2) similarities between feeding larvae are believed to indicate descent from a common planktotrophic ancestor (Strathmann 1993); and (3) theory predicts that the loss of the complex larval features associated with feeding will be irreversible (Strathmann 1993; Wray 1996). In this context, Davidson *et al.* (1995; see also Peterson *et al.* 1997, 2000) proposed the 'set-aside' theory. In this theory set-aside cells (the cells that form the rudiment that gives rise to the adult body plan at metamorphosis) first evolved in sexually mature forms that resembled planktotrophic larvae, allowing the evolution of a new second life phase, namely benthic adults. The authors also argued that the evolution of set-aside cells could account for the Cambrian 'explosion' as they could be

utilized to produce the sudden appearance of macroscopic (and therefore readily fossilized) adult forms.

The set-aside theory is appealing because it provides a developmental explanation for the Cambrian 'explosion'. It has, however, been the subject of a number of convincing criticisms: (1) the theory presents functional difficulties (Wolpert 1999; Budd & Jensen 2000; Conway Morris 2000); for example, what is the selective advantage of features that are useful in large benthic adults but not in small planktotrophic larvae that would allow them to evolve in set-aside cells before they 'knew' that they were to form an adult?; (2) the set-aside theory requires indirect development to lie at the base of the Bilateria. Davidson *et al.* (1995) and Peterson *et al.* (1997) provided cladograms onto which indirect development was mapped in support of their hypothesis, but, as Jenner (2000) has pointed out, neither allows the primitive bilaterian mode to be unequivocally determined. In fact, in most recent phylogenetic analyses (e.g. Jondelius *et al.* 2002; Telford *et al.* 2003) acoel flatworms, which are directly developing, are basal among bilaterians suggesting that direct development is the primitive condition for this clade with indirect development being derived independently in several clades (Peterson *et al.* 2005); and (3) the improbability of similarities in larvae and set-aside cells evolving convergently is an argument in favour of set-aside theory, but the theory also requires that all the macroscopic adult body plans and their gene patterning systems evolved convergently (Sly *et al.* 2003). While we currently have no way to objectively decide which set of convergences are more likely to evolve (Sly *et al.* 2003), it seems that convergence is common among larval characters (e.g. Smith *et al.* 1995; Hart 2000; Rouse 2000). Dunn *et al.* (2007) showed that the development of the apical tuft, a uniquely larval feature that is present in both proterostomes and deuterostomes, is controlled by very different gene regulatory networks in a deuterostome (sea urchin) and a proterostome (gastropod), suggesting that these features represent convergent evolution.

The arguments discussed so far in this section are theoretical, rather than being based on the direct observation of ancient embryos and larvae. The fossil record represents the only way in which we can take this approach. Fossil embryos hitherto described all either represent directly developing forms or are of a large size that, by comparison to modern embryos, suggests direct development. Conway Morris (1998) has suggested that this may be evidence for direct development being primitive among bilaterians. However, now that some of these fossils have better phylogenetic constraint (Bengtson & Yue 1997; Yue & Bengtson 1999; Dong *et al.* 2004, 2005; Donoghue *et al.* 2006b), they are seen to lie in positions on the metazoan tree where direct development is expected (Dong *et al.* 2004, 2005). In addition, it is not yet clear if the fossil record of embryos is biased towards larger more robust direct developers (see section 1.2.2).

Nützel *et al.* (2006) used the fact that the embryonic shell of molluscs is present in the adult as the protoconch (e.g. Jablonski & Lutz 1983; see Section 1.2.2) to study their developmental strategy in the Palaeozoic. They found only non-planktotrophs in the Cambrian with planktotrophy evolving approximately at the Cambrian-Ordovician boundary (Nützel *et al.* 2006; see also Freeman & Lundelius 2007; Runnegar 2007; Nützel *et al.* 2007). This timing concurs with indirect evidence for a lack of Cambrian planktotrophs from both the lack of the large adult body size required for planktotrophy in the Cambrian (Chaffee & Lindberg 1986), and the scarcity of epifaunal suspension feeders in the Cambrian (Signor & Vermeij 1994; Peterson 2005). Furthermore, it is in agreement with molecular clock evidence presented by Peterson (2005) that argues for the evolution of planktotrophy in various clades at the Cambrian-Ordovician boundary. In contrast, Freeman & Lundelius (2005) found that most early Palaeozoic brachiopods had planktotrophic development. However, as Nützel *et al.* (2006) pointed out, this study only included a few Cambrian specimens.

In summary, it seems to me that the balance of evidence currently available from molecular clocks, functional morphology and palaeontology favours the idea that direct development is the primitive state in bilaterians. It therefore seems most likely that larval stages arose gradually by intercalation into the early stages of a directly developing strategy (Wolpert 1999; Valentine & Collins 2000). Sly *et al.* (2003) proposed a realistic series of events by which this could have happened with each stage being selectively advantageous. Under this scheme set-aside cells would have evolved convergently in the latter stages of the evolution of indirect development allowing rapid and complete metamorphosis. Thus it seems that the shifts from planktotrophy to non-planktotrophy in the late Mesozoic studied in this thesis may in fact represent the secondary re-evolution of non-planktotrophy.

1.3 SPATANGOID SEA URCHINS AS MODEL ORGANISMS

1.3.1. Introduction to Spatangoida

The spatangoids are represented by around 350 extant species (Villier & Navarro 2004), which represents approximately one quarter of all extant echinoid species and makes them the most diverse sea urchin order in the modern oceans (Stockley *et al.* 2005). They predominantly live infaunally, inhabiting a wide range of sediment types (Ghiold 1988; Ghiold & Hoffman 1989), water depths (Mortensen 1950, 1951) and latitudes (Ghiold & Hoffman 1989) and feeding on detritus or by digesting organic matter from ingested sediment. Their adaptation to a burrowing mode of life is thought to have been the key to the success of the group (Kier 1974) as it provides access to new food supplies and a means of escape from predation (Smith 1984). They originated in the earliest Cretaceous and their rigid test and tendency to inhabit areas of active sedimentation means they have a good fossil record (Smith 1984); Villier & Navarro (2004) estimated that there are

approximately 1700 extinct species. The high quality of the spatangoid fossil record has led common taxa, such as *Micraster* (well known from the Chalk of southern England), to become the subjects of classic evolutionary studies (e.g. Rowe 1899; Stokes 1975; Smith 1984).

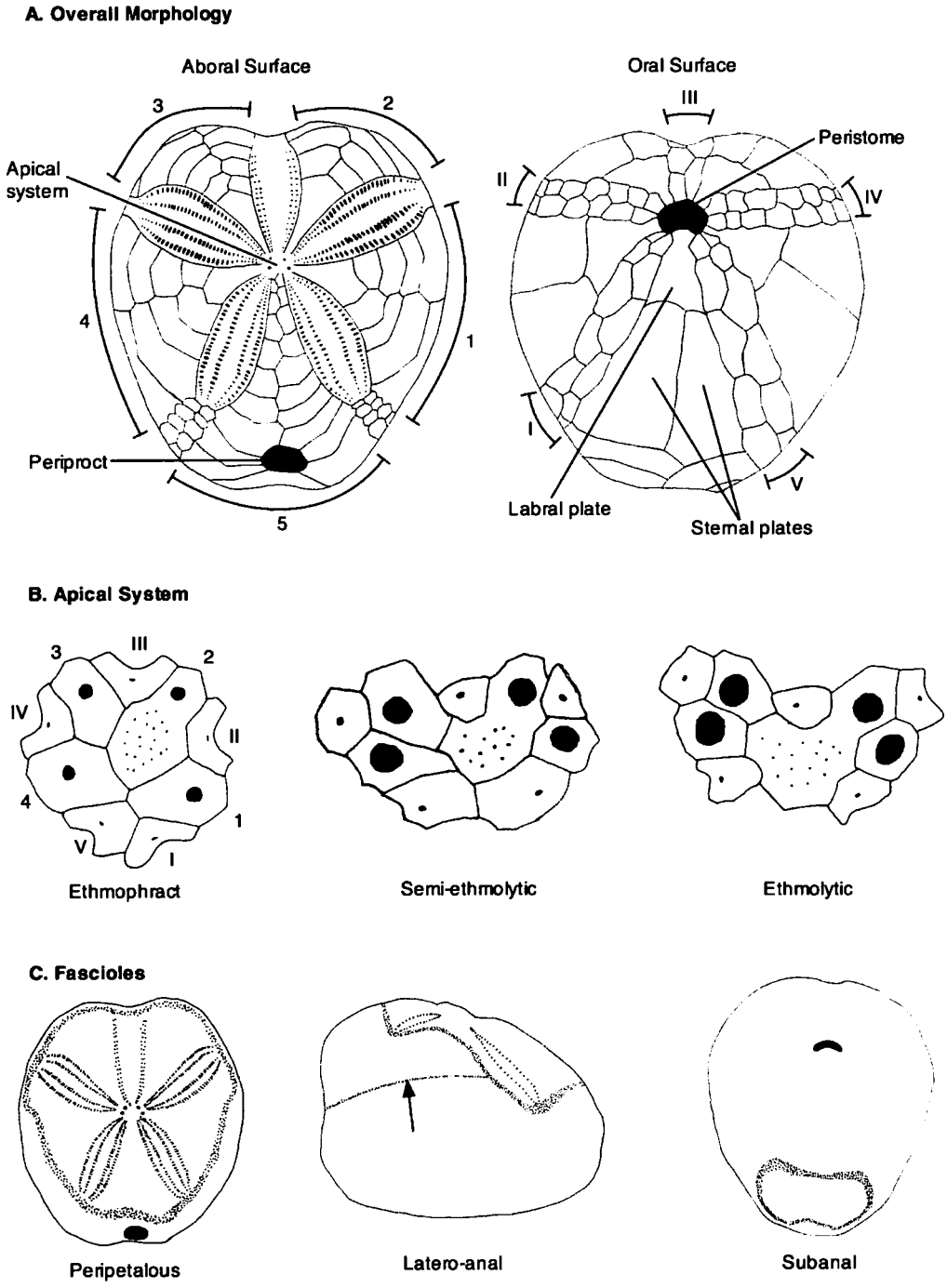

Figure 1.2: The morphology of spatangoid echinoids. (**A**) Overall morphology and main morphological terms with ambulacra numbered I-V and interambulacra 1-5; (**B**) Apical system plating with genital plates numbered 1-4 and ocular plates I-V and showing the main types of apical sytem in spatangoids: ethmophract (genital plates 1 and 4 not separated by genital plate 2), semi-ethmolytic (genital plates 1 and 4 are separated by genital plate 2, but ocular plates I and V are not), and ethmolytic (genital plates 1and 4 and ocular plates I and V are separated by genital plate 2); (**C**) The major types of fasciole in spatangoids.

Spatangoids are heart urchins: sea urchins with obvious bilateral symmetry and an anterior mouth. The spatangoids are distinguished from the other major group of heart urchins, the holasteroids, by having compact apical systems in which the four genital plates are in contact with one another. Figure 1.2 illustrates the morphology and diversity of the group. The history of classification and taxonomy of the spatangoids are discussed in detail in Chapter 2.

1.3.2. Why is it an ideal study group?

The Cretaceous spatangoid sea urchins represent an ideal group for this kind of study for a number of reasons. Firstly, a technique has been developed whereby the crystallography of the plates of the apical system can be used to unambiguously infer the developmental strategy of sea urchins (Emlet 1985, 1989; see section 4.2). Spatangoids are commonly preserved as fossils and, unlike some other sea urchin groups, the apical system is usually present (whereas in some other groups the apical system tends to separate from the corona soon after death). In the Cretaceous they lived in a wide range of environments from the equator to the poles, making them useful for studies of the relationship between developmental mode and palaeoenvironmental and palaeobiogeographical factors. They have relatively complex morphology and it is therefore relatively straightforward to resolve their phylogenetic relationships using cladistic methodology. Finally, the Cretaceous spatangoids are known to contain both planktotrophic and non-planktotrophic species and span the period when non-planktotrophic larvae are thought to have first evolved in sea urchins.

1.4. THE AIMS OF THIS PROJECT

The overall aims of the work presented in this thesis are: to investigate the number, timing and direction of switches in developmental strategy in the Cretaceous spatangoid sea urchins and to assess the relationship between developmental strategy and macroevolutionary, palaeoenvironmental and palaeobiogeographical factors.

Chapter 2 presents a taxonomic revision of the Cretaceous members of the spatangoid families Hemiasteridae, Micrasteridae, Aeropsidae, Schizasteridae and Somaliasteridae. The Toxasteridae were excluded due to constraints of time and the fact that crystallographic analysis of members of each toxasterid genus revealed no examples of non-planktotrophy. Such a taxonomic study is a pre-requisite to any study of involving species turnover as non-standardized taxonomy can skew the results of such studies. This is because events treated as extinction or speciation events using a non-standardized taxonomy may actually simply reflect artefacts of taxonomic naming (e.g. Smith & Jeffery 2000).

Chapter 3 contains phylogenetic analyses of the species that are considered valid in the taxonomic revision of the previous chapter. These analyses use standard cladistic methodology to produce hypotheses of evolutionary relationships from morphological data (see e.g. Smith 1994 for summary of cladistic methodology). The resulting hypotheses form the basis for the analyses of the evolution of developmental strategies in the subsequent chapters.

Chapter 4 addresses the timing, direction and location of switches in developmental strategy in Cretaceous spatangoids and assesses whether switches in larval mode are scattered randomly through time and space or concentrated in particular regions or stratigraphic horizons.

Chapter 5 assesses the relationship between developmental strategy and such factors as speciation rate, extinction rate, species longevity, geographical range, latitude and palaeoenvironment. Comparative methodology is used because it is important that evolutionary history is considered when carrying out analyses such as these. This is because sister species are likely to share similar traits (such as geographical range) as a result of their shared evolutionary history, and so they are not truly independent. Treating species as independent data points is therefore flawed and can lead to spurious correlations. Phylogenetic comparative methods (e.g. Harvey & Pagel 1991) such as *independent contrasts* (Felsenstein 1985), which is the method used here, aim to take shared ancestry into account.

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2. A TAXONOMIC REVISION OF THE CRETACEOUS SPATANGOIDS

2.1 INTRODUCTION

The recent spatangoids are divided into three major clades: the Paleopneustina, Hemiasterina and Micrasterina. These clades have been distinguished largely on the basis of the pattern of fascioles (bands of ciliated spines) that they bear and the plating of the apical system.

Paleopneustina has been used for taxa that have a marginal or latero-anal fasciole that passes along the margin of the test and beneath the anus; an additional peripetalous fasciole that passes around the tips of the petals may also be present. Hemiasterina has been used for taxa bearing only a peripetalous fasciole, while Micrasterina has been used for those that only have a subanal fasciole, which forms a closed loop beneath the anus. Paleopneustina has been defined as having an ethmolytic apical sytem in which genital plate 2 separates the posterior genital and ocular plates. Hemiasterina and Micrasterina, on the other hand, have been defined as having an ethmophract apical system where both the posterior genitals and oculars are in contact with one another.

The taxonomy of the Cretaceous members of the spatangoid clade is revised in this chapter. This provides a standardized taxonomic scheme for the group that is used in the analyses in the chapters that follow, meaning that we can have greater confidence that speciation and extinction events represent genuine biological phenomena rather than artefacts of taxonomic naming.

2.2 HISTORY OF CLASSIFICATION

Mortensen's (1950, 1951) classification included three major groupings of spatangoids based on plastron structure; these are: Protosternata (labral

plate followed by undifferentited biserial plating), Meridosternata (labral plate followed by a single sternal plate) and Amphisternata (labral plate followed by two prominent sternal plates divided by a roughly straight suture). However, Durham & Melville (1957) restricted the spatangoids to include only amphisternous forms and placed the other two groups in Holasteroida. All subsequent workers have followed this restricted usage of Spatangoida (Stockley *et al.* 2005).

Mortensen (1950, 1951) divided the amphisternous forms into families almost entirely on the basis of the plating of the apical system and the types of fasciole present, but he did not place these families into any higher taxonomic scheme. In the *Treatise on Invertebrate Paleontology* Fischer (1966) produced a taxonomy that closely followed Mortensen's at family level, but divided the eleven families into four suborders. These four suborders are: Toxasterina (petaloid spatangoids with no fascioles and an ethmophract apical system; includes only Toxasteridae), Hemiasterina (spatangoids with a peripetalous fasciole but no subanal fasciole, apical system usually ethmophract; includes Hemiasteridae, Schizasteridae, Aeropsidae and three post-Cretaceous families), Micrasterina (spatatangoids with a subanal fasciole, apical system usually ethmophract), and Asterostomatina (apetaloid spatangoids with no fascioles; this group contains only the post-Cretaceous family Asterostomatidae, which is equivalent to Mortensen's Paleopneustidae).

Chesher (1968) realized that *Paleopneustes*, which had been placed in Asterostomatidae, and the family Pericosmidae, which had been placed in Hemiasterina, had fascioles that were identical. As a result he synonymized Paleopneustidae and Pericosmidae and transferred the majority of taxa that Mortensen had assigned to Paleopneustidae to Asterostomatidae. Markov & Solovyev (2001) argued that the paleopneustid marginal fasciole is

homologous with the latero-anal fasciole of schizasterids. They therefore placed both families in a clade named Paleopnustoidea.

The advent of phylogenetic analysis has led to a number of modifications to the taxonomic scheme for spatangoids. Firstly, Jeffery (1999) used cladistic analysis to demonstrate that the family Somaliasteridae, which had previously been assigned to the holasteroids, belonged to the spatangoid clade.

Villier *et al.* (2004) carried out a detailed analysis of early Cretaceous taxa in order to understand the early radiation of the spatangoids. Their analysis found that the toxasterids represent a basal grade and found support for monophyletic Micrasterina and Hemiasterina clades.

Stockley *et al.* (2005) carried out morphological phylogenetic analysis of 88 fossil and living genera as well as molecular analysis of a subset of 21 of the extant genera. This study included fasciole pathway characters, which Smith & Stockley (2005) had shown to be a source of important phylogenetic information, and led to a number of important taxonomic conclusions:

- Toxasteridae is recovered as a basal grade.
- Asterostomatidae is, as Fischer (1966) suspected, a polyphyletic group.
- There was no support for a monophyletic Hemiasterina, unlike in the Villier *et al.* (2004) analysis; instead it represented a paraphyletic grouping.
- Schizasterids form two clades based on their fasciole pathways; these are Schzasteridae and Prenasteridae.
- Schizasterids, prenasterids and paleopneustids share a common fasciole pathway and form a clade named Paleopneutidea.

Despite the work described above the classification of the Cretaceous spatangoids is in need of revision (though Smith & Jeffery (2000) made significant inroads with their revision of the Maastrichtian taxa). The remainder of this chapter aims to provide such a revision. As noted in Section 1.4, the Toxasteridae are not included in this revision due to constraints of time and to the fact that a broad survey revealed no examples of non-planktotrophy.

In the systematic palaeontology of that follows I provide a diagnosis for each genus and list the type species. For genera with type species that are not found in the Cretaceous I also include the occurrence of the type species. I then list the Cretaceous species that I consider to be valid. I provide a synonymy list for each species; this is not intended to be exhaustive as it includes only type specimens and Cretaceous specimens. A diagnosis and listing of known occurrences is also given.

2.3 FAMILY AEROPSIDAE

The aeropsids are an unusual group of spatangoid echinoids that are today known only from two species of the deep-water genus *Aeropsis*. They are characterized by having paired ambulacra that are virtually flush and apetaloid to sub-petaloid, and narrow elongate plastrons in which the labral plate is approximately equal in length to the sternal plates. Until recently there were no unequivocal aeropsids known from the fossil record. However, the discovery of the Palaeocene genus *Sphenaster* Jeffery in Smith *et al.*, 1999 not only represented the first definite fossil aeropsid, but also linked the extant aeropsids to the extinct family Corasteridae (see Smith 2005; Kroh 2004). Smith (2005) have argued that the corasterids represent a paraphyletic grouping lying basal to *Aeropsis* plus *Sphenaster*, and they include all these taxa within Aeropsidae. I agree with this suggestion and use Aeropsidae to refer to this clade as a whole; I use the informal term

"corasterids" to refer to the paraphyletic grouping of fossil taxa previously assigned to the family Corasteridae.

The family Aeropsidae was erected by Lambert (1896), who included a large number of apetaloid taxa. These included both fossil and recent genera some of which were spatangoids and some holasteroids. Mortensen (1950 p. 326) considered the group to be "a real balderdash" and he revised it to include only the genera *Aeropsis*, *Aceste* (now considered a schizasterid; see below) and *Cottreaucorys* (now considered a corasterid e.g. Smith & Jeffery 2000).

Lambert & Thiéry (1924) erected the tribe Corasterinae; this included Cretaceous and Palaeocene taxa that differ from *Sphenaster* and *Aeropsis* only in the shape of the test and in having smaller pore-pairs in the anterior ambulacrum, which is flush (rather than sunken) close to the apical system. Smith (2005) suggested the corasterids were a paraphyletic basal grade within the aeropsids and this finding is supported by the phylogenetic analysis of Stockley *et al.* (2005), which includes some aeropsid taxa. Kroh (2004) argued that it is likely that *Sphenaster* and the extant aeropsids evolved from the corasterids by the acquisition of a subanal heel, elongation of the test and specialization of the tube feet in the anterior ambulacrum. He also suggested that the genus *Cottreaucorys*, which has a pronounced subanal heel but small pore-pairs in the anterior ambulacrum, provides a link between the corasterids and *Aeropsis* plus *Sphenaster*.

Smith & Jeffery (2000) provided a detailed revision of the Maastrichtian and Palaeocene aeropsids, which included placing *Cottreaucorys* under the synonymy of *Coraster*. In spite of this work the taxonomy and phylogeny of the group as a whole is in need of review. Here I provide a revision of the taxonomy of the Aeropsidae. The few post-Cretaceous species are included for completeness.

Family **AEROPSIDAE** Lambert, 1896

DIAGNOSIS

Paired ambulacra non-petaloid to sub-petaloid, more or less flush. Apical disc ethmophract to semi-ethmolytic. Plastron narrow, elongate and amphisternous with labrum approximately the same length as the sternal plates. Peripetalous fasciole usually present, highly oblique, passing subambitally around the anterior; no other fascioles.

KEY TO GENERA

1. Test wedge-shaped to cylindrical; anterior ambulacrum with enlarged, differentiated pore-pairs. Go to 2.

   Test sub-conical to sub-globular; anterior ambulacrum with small rudimentary pore-pairs. Go to 3.

2. Test cylindrical, extremely elongate; peristome closer to the mid-length than to the anterior margin of the test. *Aeropsis.*

   Test wedge-shaped; peristome anterior. *Sphenaster.*

3. Sub-conical test; ambulacral plates more than twice as wide as high. *Homoeaster.*

   Globular or sub-globular test; ambulacral plate width less than 1.5 times height. Go to 4.

4. Three gonopores. *Orthaster.*

   Four gonopores. Go to 5.

5. Test with pronounced sub-anal heel. *Cottreaucorys.*

   Test without pronounced sub-anal heel. *Coraster.*

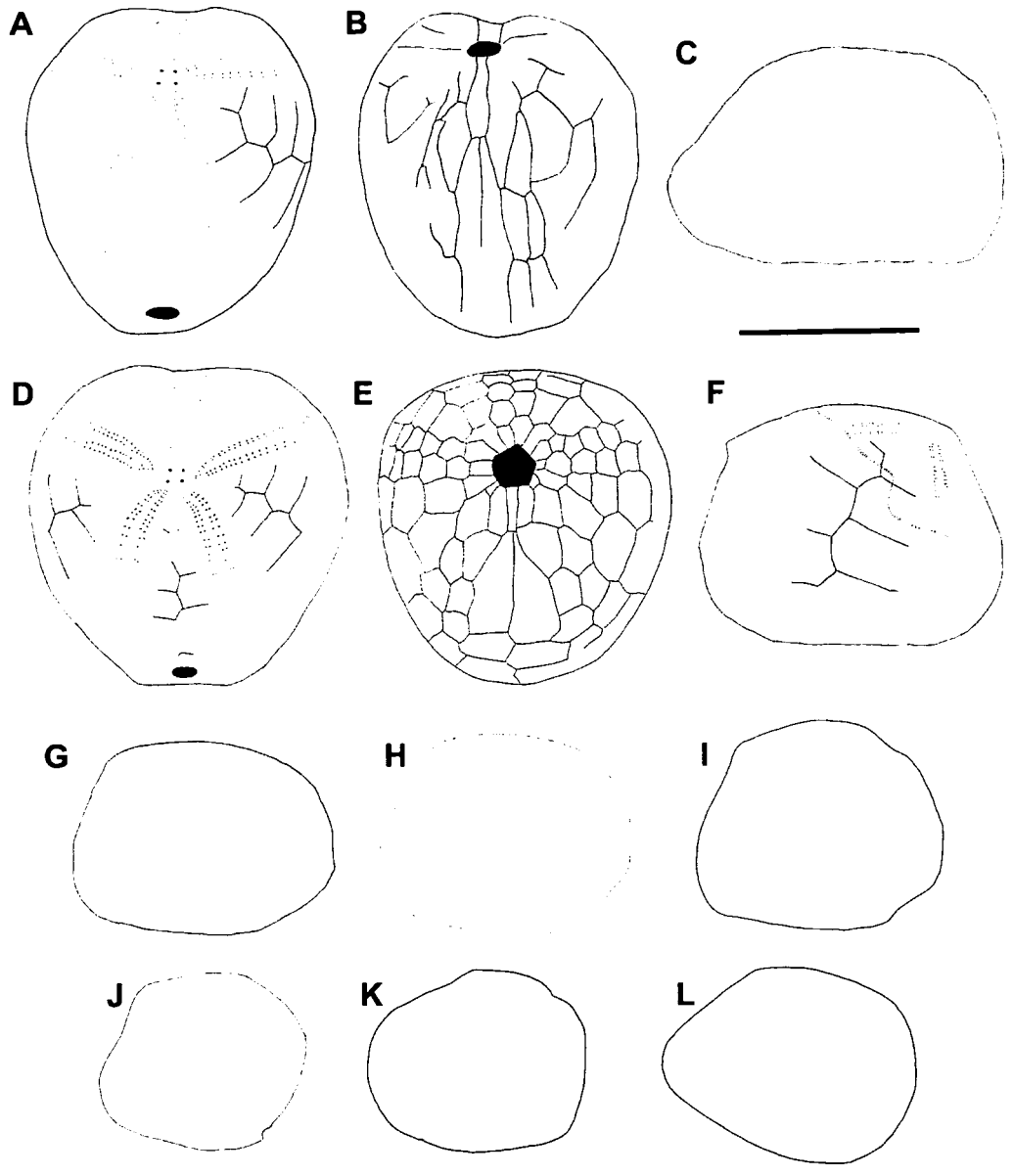

Figure 2.3.1: Aeropsidae. (**A-C**) *Cottreaucorys blayaci* (A) BMNH EE8392, Maastrichtian of Alicante, Spain, apical view; (B) same specimen, oral view; (C) MNHN J06071, syntype, Bjord Sabath, Algeria, lateral view; (**D**) *Homoeaster auberti* BMNH EE8388, Maastrichtian of Aspe, Alicante, Spain, apical view; (**E**) *Homoeaster inflatus* MNHN J01094, Maastrichtian of Senegal, oral view; (**F**) *Homoeaster auberti* MNHN J01455, syntype, 'Upper Senonian' of Djebel Ben Neja, Algeria, lateral view; (**G-L**) Lateral views of a series of specimens from the Maastrichtian of Alicante, Spain that form a transition from *Coraster* to *Cottreaucorys*: (G) BMNH EE8394 (H) BMNH EE8390 (I) BMNH EE8392 (J) BMNH EE8391 (K) BMNH EE8395 (L) BMNH EE83132. Relative scale bar: (A) 11.7 mm (B) 11.7 mm (C) 13.8 mm (D) 16.5 mm (E) 16.2 mm (F) 12.33 mm (G) 11.4 mm (H) 15.8 mm (I) 16.4 mm (J) 14.6 mm (K) 15.2 mm (L) 16.0 mm.

Genus AEROPSIS Mortensen, 1907

TYPE SPECIES

Aerope rostrata Thomson 1877, p. 211, by original designation.

DIAGNOSIS

Extremely elongate cylindrical test. Apical system anterior with one to two genital plates that are perforated by two or four gonopores. Anterior ambulacrum with differentiated pore-pairs adapicaly; depressed close to the apical system, but flush at ambitus and on oral surface. Peristome central, faces downwards. Periproct on aboral surface.

REMARKS

Aeropsis is easily distinguished by its distinctive elongate cylindrical test. It is closest to *Sphenaster*, which differs in having a wedge-shaped test, a lower periproct and a more anterior mouth that is inclined forwards, rather than downwards.

Aeropsis rostrata (Thomson, 1877)

1877 *Aerope rostrata* Thomson, in Jefferys, p. 211
1878 *Aerope rostrata* Thomson, p. 353; text-fig. 99.
1881 *Aerope rostrata* Thomson; Agassiz, p. 192, pl. 33; pl. 33a: figs 8-12

DIAGNOSIS

Apical system with two gonopores (the anterior pores absent); plates 1 and 2 are fused together as are plates 3 and 4, which results in one plate on either side of the apical system.

OCCURRENCE

Recent, North Atlantic (Jefferys 1877; Thomson 1878).

Aeropsis fulva (Agassiz, 1898)

1898 *Aerope fulva* Agassiz, p. 81; pl. 8: figs 5-6

DIAGNOSIS

Apical system with four gonopores, possibly monobasal.

OCCURRENCE

Recent, East and North Pacific (Agassiz 1898).

REMARKS

Aeropsis rostrata and *A. fulva* differ mainly in the structure of the apical disc. *Aeropsis rostrata* has two gonopores with the plates fused into a single plate on either side; *A. fulva* has four genital pores, in the illustration of the holotype provided by Smith (2005) it appears that all four genital plates may be fused into a single plate.

Genus CORASTER Cotteau, 1886

TYPE SPECIES

Coraster villanovae Cotteau, 1886, by monotypy.

DIAGNOSIS

Test sub-globular without marked sub-anal heel. Apical system anterior with four gonopores. Ambulacral plates high: less than 1.5 times wider than high. Peripetalous fasciole passing close to the high point of the test in the posterior interambulacrum.

REMARKS

The species of this genus represent a paraphyletic grouping in the phylogenetic analysis presented herein, but it is retained here nevertheless as I consider it to be a useful grouping. Differs from *Orthaster* in having four, rather than three, genital pores. Differs from *Homoeaster* in having a more gibbous profile and higher ambulacral plates. Differs from *Cottreaucorys* in lacking a prominent sub-anal heel.

Coraster vilanovae Cotteau, 1886

1886 *Coraster vilanovae* Cotteau, p. 70; pl. 9: figs 1-4
1888 *Coraster marsooi* Seunes, p. 806; pl. 29: fig. 2
1888 *Coraster sphaericus* Seunes, p. 807; pl. 29: fig. 3
1888 *Coraster munieri* Seunes, p. 808; pl. 29: fig. 4
1892 *Coraster vilanovae* Cotteau; Nicklès, p. 115
1892 *Coraster marsooi* Seunes; Nicklès, p. 115
1892 *Coraster munieri* Seunes; Nicklès, p. 115
1899 *Coraster vilanovae* Cotteau; Anthula, p. 61; pl. 2: fig. 5
1927 *Coraster vilanovae* Cotteau; Böhm, p. 195; pl. 12: fig. 6
1927 *Coraster frechi* Böhm, p. 195; pl. 12: fig. 5
1931 *Coraster vilanovae* Cotteau; Lambert, p. 8; pl. 1: fig. 16
1931 *Coraster alapiensis* Lambert, p. 9; pl. 1: figs 10-11
1934 *Coraster vilanovae* Cotteau; Tzankov, p. 210
1937 *Coraster* sp. Lambert & Charles, p. 388; pl. 8: fig. 4
1940 *Coraster* cf. *sphaericus* Seunes; Rouchadzé, p. 170; pl. 1: fig. 4
1940 *Coraster munieri* Seunes; Rouchadzé, p. 170
1959 *Coraster caucasicus* Mosvkin & Poslavskaya, p. 276; pl. 18: fig. 3; text-fig. 87
1959 *Coraster cubanicus* Mosvkin & Poslavskaya, p. 277; pl. 18: fig. 4; text-fig. 88
1959 *Coraster vilanovae* Cotteau; Moskvin & Poslavskaya, p. 278; pl. 18: fig. 5; text-fig. 89

1959 *Coraster sphaericus* Seunes; Moskvin & Povlavskaya, p. 278; pl. 18: fig. 6; text-fig. 90

1959 *Coraster ansaltensis* Poslavskaya, in Moskvin & Povlavskaya, p. 279; pl. 18: fig. 7; text-fig. 91

1960 *Coraster vilanovae* Cotteau; Poslavskaya & Moskvin, p. 65; pl. 4: fig. 1; text-fig. 15

1960 *Coraster sphaericus* Seunes; Poslavskaya & Moskvin, p. 65; pl. 4: fig. 2; text-fig. 16

1960 *Coraster ansaltensis* Poslavskaya; Poslavskaya & Moskvin, p. 66; pl. 4: fig. 3; text-fig. 17

1964 *Coraster vilanovae* Cotteau; Poslavskaya & Solovyev, p. 183, pl. 34: fig. 9

1979 *Coraster* cf. *vilanovae* Cotteau; Gongadze, p. 117; pl. 27: fig. 1

1979 *Coraster sphaericus* Seunes; Gongadze, p. 119; pl. 27: fig. 2

1979 *Coraster ansaltensis* Poslavskaya; Gongadze, tables 1-2

1995 *Coraster vilanovae* Cotteau; Gallemí *et al.*, table 1

1995 *Coraster* sp. Gallemí *et al.*, table 1

1995 *Coraster vilanovae* Cotteau; Mileva-Ilieva p. 238; pl. 2: figs 7-9

1999 *Coraster vilavovae* Cotteau; Smith *et al.*, pl. 11: figs 4-7; text-fig. 37a

2000 *Coraster vilanovae* Cotteau; Smith & Jeffery, p. 355-356; text-fig 146.

2001 *Coraster vilanovae* Cotteau; Kroh, p. 414; pl. 14: figs 1-6; text-figs 27-29

DIAGNOSIS

Globular test with frontal groove weak or absent; circular to ovate in horizontal outline. Apical system usually ethmophract. Position of mouth extremely variable: from one quarter of test length from anterior margin to almost marginal.

OCCURRENCE

Maastrichtian of Alicante, Spain (Gallemí *et al.* 1995); Danian of Navarra (Smith *et al.* 1999); Maastrichtian of Bulgaria (Mileva-Ilieva 1995); Maastrichtian and Danian of Turkey (Böhm 1927; Lambert 1931); Maastrichtian of the Transcaspian (Poslavskaya & Mosvkin 1960); Maastrichtian to Danian of Georgia (Rouchadzé 1940; Poslavskaya & Mosvkin 1960; Gongadze 1979) and Caucasus (Mosvkin & Poslavskaya 1959; Poslavskaya & Mosvkin 1960); Maastrichtian and Palaeocene of Dagestan (Anthula 1899; Mosvkin 1982). Also from the Danian of Austria (Kroh 2001) and French and Spanish Pyrenees (Plaziat *et al.* 1975).

REMARKS

Historically species of *Coraster* have been distinguished on the basis of subtle features of test shape, frontal groove depth and position of the peristome. However, as Smith & Jeffery (2000) noted, there are gradational series between these varieties and I therefore treat them as synonyms. The only exception is *C. beneharnicus*, which lies outside this range of variability and can be distinguished by its more elongate and angular test, its weak sub-anal heel and its frontal groove that extends to the peristome.

Coraster beneharnicus Seunes 1888

1888 *Coraster beneharnicus* Seunes, p. 804; pl. 29: fig. 1

1975 *Coraster beneharnicus* Seunes; Plaziat *et al.*, p. 635; pl. 1: figs 1-6; text-figs 6,8

1999 *Coraster beneharnicus* Cotteau; Smith *et al.*, pl. 11: figs 1-5; text-fig. 37b

1999 *Coraster vilanovae* Cotteau, Jagt, p. 8

2000 *Coraster beneharnicus* Seunes; Smith & Jeffery, p. 356

2004 *Coraster beneharnicus* Seunes; Kroh & Jagt, p. 556; pl. 5: figs 4-7; text figs 10, 11

DIAGNOSIS

Test elongate and angular in horizontal outline with weak sub-anal heel. Broad, shallow frontal groove which extends to the peristome. Apical system usually semi-ethmolytic. Peristome situated at approximately one quarter of the total test length from the anterior margin.

OCCURRENCE

Maastrichtian of Alicante (BMNH); Austria, precise age uncertain (Jagt 1999; Kroh & Jagt 2004). Also from the Danian of the French and Spanish Pyrenees (Seunes 1888; Plaziat *et al.* 1975); Danian of Navarro, Spain (Smith *et al.* 1999).

Genus COTTREAUCORYS Lambert, 1920b

TYPE SPECIES

Homoeaster blayaci Cottreau in Blayac & Cottreau, 1909, by original designation.

DIAGNOSIS

Test with pronounced sub-anal heel and supra-marginal peristome. Apical system with two or four gonopores. Ambulacral plates high: less than 1.5 times wider than high. Peripetalous fasciole passing close to the high point of the test in the posterior interambulacrum.

REMARKS

Smith & Jeffery (2000) placed this genus under the synonymy of *Homoeaster*, but Kroh (2004) and Smith (2005) both considered *Cottreaucorys* to be sufficiently distinct as to merit a separate genus. I consider *Cottreaucorys* to be closer to *Coraster* than to *Homoeaster* because *Cottreaucorys* and *Coraster* both exhibit wider ambulacral plates and a peripetalous fasciole that passes close to the high point of the test.

Furthermore, a series of specimens from Alicante, Spain (BMNH EE 8132 and EE 8390-8395; see figure 2.3.1) appear to show variable development of the heel from *Coraster beneharnicus* to *Cottreaucorys blayaci*.

The phylogenetic analysis presented here supports the suggestions by Kroh (2004) that *Cottreaucorys* is the sister group to *Sphenaster* and the extant aeropsids, and that these taxa arose from the taxa previously assigned to the corasterids by the development of the heel and specialization of the tube feet of the anterior ambulacrum. Although the species of this genus represent a paraphyletic grouping in the phylogenetic analysis presented herein, it is nevertheless retained here as I consider it to be a useful grouping.

Cottreaucorys blayaci (Cottreau in Blayac & Cottreau, 1909)

Figure 3.2.1 A-C

1909 *Homoeaster blayaci* Cottreau in Blayac & Cottreau, p. 428; pl. 14: figs 7-19
1932 *Cottreaucorys blayaci* (Cottreau); Lambert, p. 76
?1971 *Cottreaucorys (Homoeaster) blayaci* (Cottreau); Akkus, p. 16
?2000 ?*Homoeaster* sp. indet. 1, Smith & Jeffery, p. 361

DIAGNOSIS
Strongly pronounced sub-anal heel. Apical system with four genital plates and four gonopores.

OCCURRENCE
Maastrichtian of Spain (BMNH), North Africa (Cottreau in Blayac & Cottreau 1909; Lambert 1932) and possibly Turkey (Akkus 1971; this material is not figured and I have not studied the original specimens).

Cottreaucorys kollmani Kroh, 2004

2004 *Cottreaucorys kollmani* Kroh, p. 313; pl. 1: figs 1a-d; text-fig. 2: figs 1a-d

DIAGNOSIS

Apical system with two gonopores and with plating reduced or fused to give a single genital plate on each side of the apical system.

OCCURRENCE

Danian of Ernstbrun, Austria.

REMARKS

Cottreaucorys kollmani and *C. blayaci* differ mainly in the structure of the apical disc: while *C. blayaci* has an ethmophract apical system with each of the four genital plates perforated by a genital pore, *C. kollmani* has reduced or fused plating with only two genital plates and two gonopores. In addition, the test of *C. kollmani* is more globular and has a weaker sub-anal heel than that of *C. blayaci.*

Cottreaucorys sulcatus Nisiyama, 1968

1968 *Cottreaucorys (Cordastrum) sulcatus* Nisiyama, p. 175; pl. 18: figs 10-11; pl. 20: fig. 2

2000 *Homoeaster* sp. indet. 2, Smith & Jeffery, p. 361

DIAGNOSIS

Deep frontal groove that cuts the ambitus. Moderately well developed petals.

OCCURRENCE

Maastrichtian of Japan.

REMARKS

Differs from other *Cottreaucorys* species in having a deep frontal groove and better developed petals. These differences may be sufficient to merit a distinct genus but as the type material has not been seen as part of this study I prefer to leave it in *Cottreaucorys* pending re-study.

Genus HOMOEASTER Pomel, 1883

[=*Physaster* Pomel, 1883, type species *Holaster inflatus* Desor in Agassiz & Desor, 1847; =*Ornithaster* Cotteau, 1886, type species *Ornithaster evaristei* Cotteau, 1886; =*Inflataster* Anthula, 1899, type species *Inflataster abichi* Anthula, 1899]

TYPE SPECIES

Homoeaster tunetanus Pomel, 1883, by original designation.

DIAGNOSIS

Test sub-conical with flat oral surface. Apical system anterior with four gonopores. Ambulacral plates more than twice as wide as high. Peristome pentagonal. Peripetalous fasciole passes closer to the ambitus than to the high point of the test.

REMARKS

Physaster has been distinguished from *Homoeaster* due to its asymmetric sternal plates with an oblique suture. However, this difference is slight and I do not consider it to be of generic value; the two genera are thus synonymized. *Ornithaster* has been distinguished from *Homoeaster* on the basis of having round, rather than slightly elonongate, pores on the upper

surface no frontal sulcus. However, I consider these differences to be slight and so follow Smith & Jeffery (2000) in treating the two genera as synonyms.

Homoeaster is distinguished from other aeropsids on the basis of its sub-conical test, wide ambulacral plates and pentagonal peristome.

Homoeaster tunetanus Pomel, 1883

1883 *Homoeaster tunetanus* Pomel, p. 44
1892 *Homoeaster tunetanus* Pomel; Gauthier; p. 45; pl. 2: figs 3-10
1925 *Homoeaster petalodes* Lambert in Lambert & Thiéry, p. 429; pl. 11: figs 7-8
1959 *Homoeaster tunetanus* Pomel; Mosvkin & Poslavskaya, p. 274; pl. 18: fig. 1
1960 *Homoeaster tunetanus* Pomel; Poslavskaya & Mosvkin p. 60; pl. 3: fig. 1; text-fig. 10
1979 *Homoeaster* cf. *tunetanus* Pomel; Gongadze, p. 110: pl. 25: fig. 4
1983 *Homoeaster*? n. sp. aff. *tunetanus* Pomel; Schulz p. 718; text-fig. 3
1995 *Homoeaster tunetanus* Pomel; Mileva-Ilieva, p. 239

DIAGNOSIS
Sub-conical test with obliquely truncate posterior. Peripetalous fasciole with a marked kink behind the anterior paired petals. Relatively large, heterogeneous 'primary' tubercles.

OCCURRENCE
While this species has been reported from the Maastrichtian of North Africa, micropalaeontological data suggests that this species actually occurs in the Coniacian in Algeria and Tunisia (Zaghbib-Turki 1987); Maastrichtian-Danian of Spain (BMNH); Maastrichtian of the Caucasus, Crimea and Transcaspian region (Mosvkin & Poslavskaya 1959; Poslavskaya & Mosvkin 1960);

Maastrichtian of Georgia (Gongadze 1979); Maastrichtian of Bavaria (Schulz 1983).

Homoeaster ardouini Lambert, 1903a

1903a *Homeaster ardouini* Lambert, p. 80; pl. 3: figs 1-2
1930 *Homoeaster ardouini* Lambert; Besairie & Lambert, p. 108, pl. 10: fig. 9
1930 *Homoeaster ardouini* Lambert; Besairie, p. 232; pl. 24: figs 1-2

DIAGNOSIS
Low sub-conical test with low periproct.

OCCURRENCE
Maastrichtian of Madagascar (Lambert 1903a; Besairie & Lambert 1930).

REMARKS
Differs from all congeners in having a considerably lower test. I have not included this species in the phylogenetic analysis in the following chapter due to insufficient data.

Homoeaster auberti (Gauthier, 1892)

Figure 3.2.1 D, F

1892 *Lambertiaster auberti* Gauthier, p. 32; pl. 3: figs 4-15
1909 *Homoeaster auberti sabathensis* Cottreau in Blayac & Cottreau, p. 426; pl. 14: figs 4-6
1932 *Homoeaster auberti* Gauthier; Lambert p. 75, 99.

DIAGNOSIS

Sub-conical test with obliquely truncate posterior. Peripetalous fasciole with a marked kink behind the anterior paired petals. Relatively small, homogeneous 'primary' tubercles.

OCCURRENCE

While this species has been reported from the Maastrichtian of North Africa, micropalaeontological data suggests that this species actually occurs in the Coniacian in Algeria and Tunisia (Zaghbib-Turki 1987).

REMARKS

This species is extremely similar to *H. tunetanus*, but can be distinguished on the basis that the largest tubercles ('primary tubercles') are smaller and more homogeneous.

Homoeaster inflatus (Desor in Agassiz & Desor, 1847)

Figure 2.3.1 E

1847 *Holaster inflatus* Desor, p. 28
1854 *Holaster inflatus* Desor; d'Orbigny, p. 89; pl. 814: figs 4-5
1886 *Ornithaster evaristei* Cotteau, p. 72; pl. 9: figs 5-8
1892 *Ornithaster evaristei* Cotteau; Nicklès, p. 115
1892 *Homoeaster discrepans* Gauthier, p. 48; pl. 4: fig. 13
1893 *Physaster inflatus* (Desor); Lambert, p. 82; text-fig. 19
1889b *Coraster margaritae* Cotteau, p. 9; pl. 1: figs 3-8
1895 *Ornithaster douvillei* Cotteau & Gauthier, p. 48, 50; text-figs 1-3
1899 *Inflataster abichi* Anthula, p. 63; pl. 2: fig. 6
1910 *Physaster vasseuri* Dalloni & Lambert in Lambert, p. 808; pl. 15
1927 *Ornithaster cordiformis* Böhm, p. 196; pl. 12: fig. 3
1927 *Physaster abichi* (Anthula); Böhm, p. 197
1934 *Ornithaster cordiformis* Böhm; Tzankov, p. 212

1934 *Physaster abichi* (Anthula); Tzankov, p. 213

1936 *Physaster inflatus* (Desor); Lambert & Jacquet, p. 344; pl. 21: figs 1-3

1940 *Physaster abichi* (Anthula); Rouchadzé, p. 170

1959 *Homoeaster abichi* (Anthula); Mosvkin & Poslavskaya, p. 274; pl. 18: fig. 2

1959 *Ornithaster sokolovi* Mosvkin & Poslavskaya, p. 275; pl. 18: figs 8-9; text-fig. 84

1960 *Homoeaster evaristei* (Cotteau); Poslavskaya & Mosvkin p. 61; pl. 3: fig. 2; text-fig. 11

1960 *Homoeaster abichi* (Anthula); Poslavskaya & Mosvkin p. 63; pl. 3: fig. 3-4; text-fig. 12

1979 *Homoeaster abichi* (Anthula); Gongadze, p. 111: pl. 26: fig. 1

1986 *Physaster inflatus* (Desor); Stokes, p. 1273

1995 *Ornithaster? evaristei* Cotteau; Gallemí *et al.*, table 1

1995 *Ornithaster?* sp. Gallemí *et al.*, table 1

1999 *Homoeaster evaristei* (Cotteau); Smith *et al.*, p. 130, pl. 11: figs 1-3; text-fig. 38

2000 *Homoeaster evaristei* (Cotteau); Smith & Jeffery, p. 358-360; text-fig 148.

2001 *Homoeaster evaristei* (Cotteau); Kroh, p. 422; pl. 14: figs 7-9; text-fig. 34

DIAGNOSIS

Sub-conical test with obliquely truncate posterior. Peripetalous fasciole gently undulating behind the anterior paired petals.

OCCURRENCE

Maastrichtian and Danian of northern Spain (Gallemí *et al.* 1995; Smith *et al.* 1999); Maastrichtian to Danian of northern Caucasus (Mosvkin & Poslavskaya 1959; Poslavskaya & Mosvkin 1960); Danian of the Crimea (Mosvkin & Poslavskaya 1959); Maastrichtian of Dagestan (Anthula 1899);

Maastrichtian of Georgia (Rouchadzé 1940; Poslavskaya & Mosvkin 1960; Gongadze 1979); Danian of Turkey (Böhm 1927); Danian of Greenland (Smith & Jeffery 2000); Maastrichtian of Mozambique (Smith & Jeffery 2000); Maastrichtian or Palaeocene of Senegal (Smith & Jeffery 2000); Cenomanian of Spain (Dalloni & Lambert 1910); Maastrictian of Senegal (Stokes 1986).

REMARKS

Close to *H. tunetanus*, but differentiated on the basis of having a peripetalous fasciole that is gently undulating, rather that having a sharp kink behind the anterior paired petals.

Genus ORTHASTER Mosvkin, 1982

TYPE SPECIES

Orthaster dagestanensis Mosvkin, 1982, by original designation. Danian of the former Soviet Union.

DIAGNOSIS

Test globular. Apical system with three gonopores, genital plate 4 is unperforated. Ambulacra apetaloid with small round pore-pairs. Peripetalous fasciole passing close to the high point of the test.

REMARKS

Mosvkin (1982) established this genus for species that had previously assigned to the genus *Ornithaster* but differed markedly from the type species *O. evaristei* (which I consider to be a species of *Homoeaster*).

Orthaster is similar to *Coraster* (from which it differs only in having three rather than four gonopores). Smith (2005) suggested that future work may show that this is not a stable character on which to base a generic division.

The genus is nevertheless retained here as the two *Orthaster* species form a monophyletic grouping in the phylogenetic analysis presented in the following chapter.

Orthaster dagestanensis Mosvkin, 1982

1959 *Ornithaster munieri* (Seunes); Mosvkin & Poslavskaya, p. 276; pl. 18: fig. 11; text-fig. 86
1960 *Ornithaster munieri* (Seunes); Poslavskaya & Mosvkin, p. 63; pl. 3: fig. 5; text-fig. 13
1960 *Ornithaster marsooi* (Seunes); Poslavskaya & Mosvkin, p. 63; pl. 3: fig. 6; text-fig. 14
1979 *Ornithaster beneharnicus* (Seunes); Gongadze p. 113; pl. 26: figs 2-3
1979 *Ornithaster munieri* (Seunes); Gongadze p. 114; pl. 26: fig. 4
1979 *Ornithaster* cf. *marsooi* (Seunes); Gongadze p. 116; pl. 26: fig. 5
1982 *Orthaster dagestanensis* Mosvkin, p. 103; pl. 10: fig. 1
1982 *Orthaster okhliensis* Mosvkin, p. 105; pl. 10: fig. 3
2001 *Ornithaster dagestanensis* Mosvkin; Kroh, p. 418; pl. 13: figs 4-8; text-figs 30-32

DIAGNOSIS
Test with upper and lower surfaces inflated. Anterior ambulacrum moderatelly depressed. Peristome marginal.

OCCURRENCE
Palaeocene of Georgia (Poslavskaya & Mosvkin 1960; Gongadze 1979) , the northern Caucasus (Mosvkin & Poslavskaya 1959; Poslavskaya & Mosvkin 1960) and Austria (Kroh 2001); Late Palaeocene of Dagestan (Mosvkin 1982).

Orthaster alievi Mosvkin, 1982

1959 *Ornithaster alapliensis* (Lambert); Mosvkin & Poslavskaya, p. 275, pl. 18: fig. 10; text-fig. 85

1964 *Ornithaster alapliensis* (Lambert); Poslavskaya & Solovyev, pl. 34: fig. 8; text-fig. 219b

1982 *Orthaster alievi* Mosvkin, p. 104; pl. 10: fig. 2

2000 *Orthaster alievi* Moskvin; Smith & Jeffery, p. 358; text-fig 147c, e

DIAGNOSIS

Test with inflated upper surface and relatively flat lower surface. Anterior ambulacrum flush or only weakly depressed. Peristome anterior.

OCCURRENCE

Campanian of Dagestan (Mosvkin 1982); Maastrichtian of the northern Caucasus and Kopet Dag (Mosvkin & Poslavskaya 1959; Poslavskaya & Solovyev 1964).

REMARKS

Differs from *O. dagestanensis* in having a flatter oral surface, a less strongly depressed anterior ambulacrum , and a peristome which lies further from the anterior margin.

***Orthaster* sp.** *in* Kroh, 2001

2001 *Ornithaster* sp. Kroh, p. 421; pl. 13: figs 1-3; text-fig. 33

OCCURRENCE

Danian of Austria.

REMARKS

Kroh (2001) reported two specimens that co-occur with *O. dagestanensis* but lie outside the usual morpholoigical range for this species. They have an elongate test with a similar form to that of *Coraster beneharnicus*, but are easily distinguished by having an apical system with only three gonopores. They may well represent a new species.

Genus SPHENASTER Jeffery in Smith *et al.* 1999

TYPE SPECIES

Sphenaster larumbensis Jeffery in Smith *et al.* 1999.

DIAGNOSIS

Wedge-shaped test. Apical system anterior with two gonopores, plating unclear: possibly fused into one plate on either side. Anterior ambulacrum with differentiated pore-pairs; weakly sunken close to the apical system, but flush at the ambitus and on the lower surface. Peripetalous fasciole passing close to the high point of the test.

REMARKS

Differs from *Aeropsis* in having a wedge-shaped (rather than cylindrical) test, a more anterior peristome and a lower periproct. Differs from *Cottreaucorys* in having a higher and narrower test and an anterior ambulacrum with differentiated pore-pairs that is depressed close to the apical system, but flush at the ambitus and on the oral surface.

Sphenaster larumbensis Jeffery in Smith *et al.* 1999

1999 *Sphenaster larumbensis* Jeffery in Smith *et al.* p. 131; pl. 11: figs 8-12; text-fig. 42.

DIAGNOSIS

As for genus.

OCCURRENCE

Palaeocene (Early Thanetian) of Navarra Province, Spain (Jeffery in Smith *et al.* 1999).

2.4 FAMILY HEMIASTERIDAE

Family **HEMIASTERIDAE** Clark, 1917

DIAGNOSIS

Spatangoids with chordate test. Apical system plating variable from ethmophract to ethmolytic. Paired ambulacra petaloid. Amphisternous plastron with triangular labral plate. Peripetalous fasciole only. Upper surface tuberculation uniform with little or no granulation.

KEY TO GENERA

1. Anterior paired petals longer than posterior pair; apical system usually ethmophract. Go to 2.

   Paired petals subequal in length; ethmolytic or semi-ethmolytic apical system. Go to 7.

2. Broad, deep frontal groove with vertical or overhanging walls on the upper surface. *Proraster.*

   Frontal groove absent or shallow. Go to 3.

3. Pustular tuberculation covering test. *Leiostomaster.*

   Fine tuberculation. Go to 4.

4. Anterior paired petals approximately twice as long as posterior paired petals. Go to 5.

Anterior paired petals approximately three times as long as posterior paired petals. *Leymeriaster*.

5. Paired ambulacra strongly pinched below petal terminations as they cross the peripetalous fasciole. *Holanthus*.

Paired ambulacra not strongly pinched. Go to 6.

6. Globular test with no frontal notch. *Bolbaster*.

Wedge-shaped test with distinct frontal notch. *Hemiaster*.

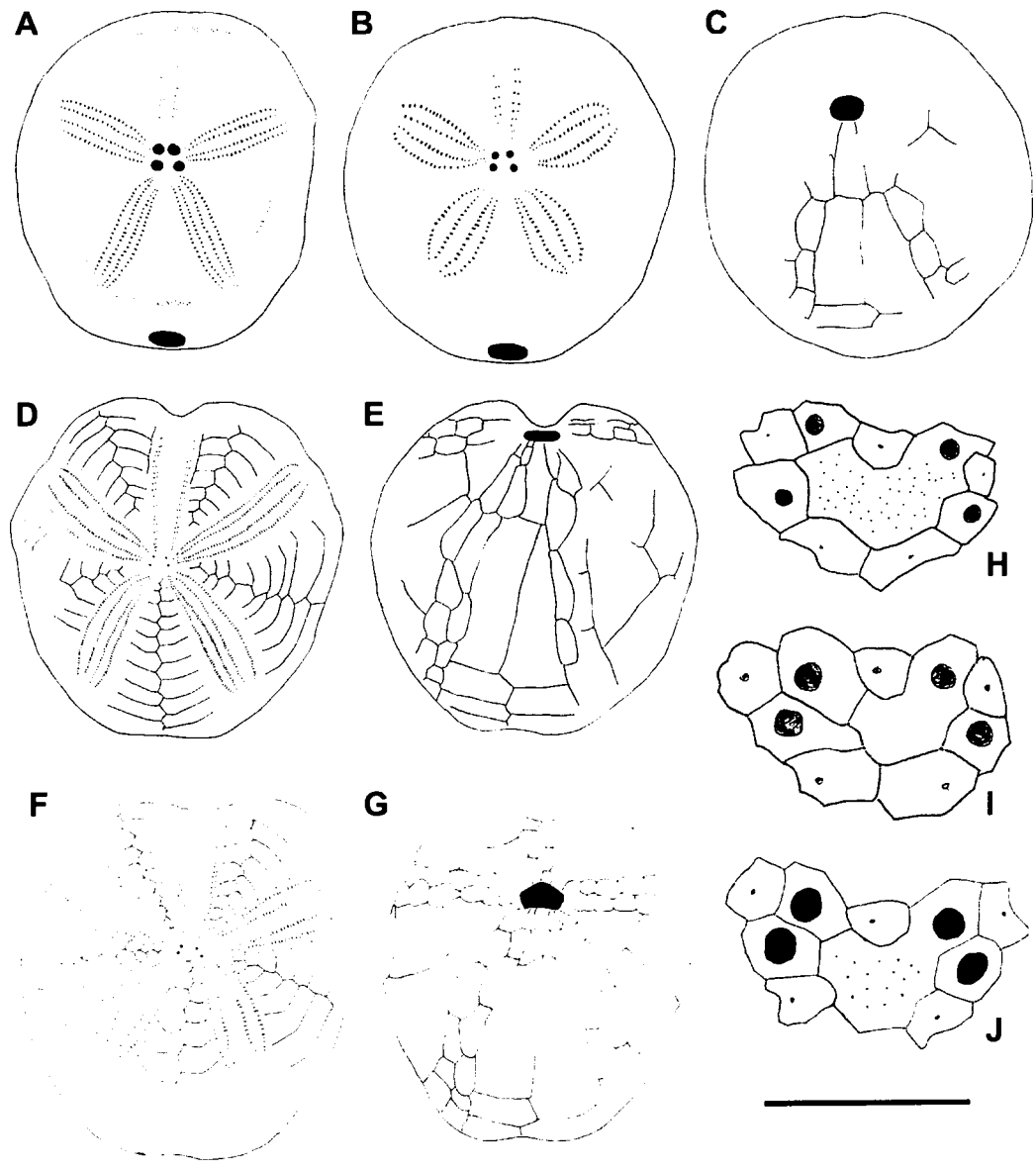

Figure 2.4.1: Hemiasteridae. (**A**) *Mauritanaster mirabilis* BMNH E3657, 'Senonian' of Kef Matrek, Algeria, apical view; (**B-C**) *Leiostomaster* sp. BMNH E79415, 1 km North of Egito, Angola, apical and oral views; (**D-E, H**) *Mecaster cubicus* (D, H) BMNH E7635, North of Hammamat Ma'in, Jordan, apical view and apical system (E) EE7637, same locality, apical view; (**F-G, I**) *Mecaster batnensis* (F, I) USNM 449382, Cenomanian of 'Bom Jesus', Sergipe, Brazil apical view and apical system, (G) USNM 449388, same locality, oral view; (**J**) *Mecaster texanus* USNM 108703, 'Senonian' of Equador, apical system. Relative scale bar: (A) 16.8 mm (B) 11.6 mm (C) 11.6 mm (D) 14.3 (E) 18.2 (F) 14.5 mm (G) 17.0 (H) 2.9 mm (I) 2.2 mm (J) 2.4 mm.

7. Paired petals flush or weakly sunken. Go to 8.
Paired petals sunken. Go to 9.

8. Paired petals practically flush. *Heterolampas.*
Paired petals weakly sunken. *Mauritanaster.*

9. Complete peripetalous fasciole. *Mecaster.*
Incomplete peripetalous fasciole present only posteriorly. *Palhemiaster.*

Genus **HEMIASTER** Desor in Agassiz & Desor, 1847

TYPE SPECIES

Spatangus bufo Brongniart, 1822 by subsequent designation of Savin, 1903.

DIAGNOSIS

Test wedge-shaped in profile with a truncate posterior; shallow, but distinct, frontal notch; two angles at posterior when viewed from above. Posterior paired petals approximately half the length of the anterior pair.

REMARKS

A large number of species have been described as members of the genera *Hemiaster* and *Bolbaster* (both considered to be subgenera of *Hemiaster* by some authors). Néraudeau (1994), for example, listed some 59 species of *Hemiaster* (*Bolbaster*) and 37 species of *Hemiaster* (*Hemiaster*). *Bolbaster* has been distinguished from *Hemiaster* by McNamara (1987) and earlier workers by having a spherical or sub-spherical test, narrow petals and practically no anterior notch. Néraudeau (1994) listed a number of other characters that distinguished *Bolbaster* (posterior apical system; flush paired petals; short labral plate; symmetrical sternal plates). Smith & Jeffery (2000) then argued that all of the features that had been used to differentiate

Hemiaster and *Bolbaster* were "not substantive and commonly size-related" (p. 320), and considered the two genera to be synonymous. However, Smith (2005) argued that the two genera could be distinguished on the basis of the plating of the oral surface with *Hemiaster* having an elongate labral plate that reaches ambulacral plate 3 and an oblique sternal suture while *Bolbaster* has a shorter labral plate and a symmetrical sternal suture.

It is certainly preferable to base generic diagnoses on clear differences in plate architecture rather than on subtleties of test shape. However, defining *Hemiaster* and *Bolbaster* on the basis of oral surface plating will inevitably lead to difficulties in practice because these features are not preserved in the type material of many of the species that belong to these genera. This would result in large numbers of species that definitely belong to either *Hemiaster* or *Bolbaster*, but that could not be assigned definitively to one or other genus due to a lack of information on the oral surface plating. As a result, the two genera are distinguished here on the basis of differences in the shape of their tests, which I do consider to be substantive – see diagnoses above and below. It should, however, be noted that these features of test shape do not always distinguish the two genera in the same way as oral plating characters do. For example *Peroniaster nasutulus* Gauthier, 1887 has a *Bolbaster*-like test shape, yet an oblique sternal suture similar to that of *Hemiaster bufo* (Brongniart, 1822), the type species of *Hemiaster*.

While some of the species listed by Néraudeau (1994) are likely to be real entities, detailed morphometric analysis of large numbers of specimens, especially those from North Africa, is required to establish the validity of these species. Such analysis is not attempted here. Instead I attempt to provide a comprehensive list of Cretaceous *Hemiaster* and *Bolbaster* specimens recorded in the literature and to place these records into

morphological groups that might prove useful to future workers attempting the kinds of analysis described above.

In the genus *Hemiaster* the differences between the numerous nominal species are often gradational and I have been unable to divide the genus into discrete morphological groups.

***Hemiaster* sp. or spp.**

1822 *Spatangus bufo* Brongniart, p. 84, 289; pl. 5: fig. 4
1829 *Spatangus bucardium* Goldfuss, p. 157; pl. 49: fig. 1
1829 *Spatangus lacunosus* Goldfuss, p. 158; pl. 49: fig. 3
1830 *Spatangus cormarinum* Morton, p. 250; pl. 3: fig. 10
1830 *Spatanus* sp. Morton, p. 286
1833 *Spatangus parastatus* Morton, p. 294
1834 *Spatangus parastatus* Morton; Morton, p. 77; pl. 3: fig. 21
1839 *Micraster minimus* Agassiz, p. 26; pl. 3: figs 16-18
1847 *Micraster globosus* Agassiz in Agassiz & Desor, p. 2
1847 *Micraster minimus* Agassiz; Agassiz & Desor, p. 122
1847 *Hemiaster amplus* Desor in Agassiz & Desor, p. 123
1847 *Hemiaster bucardium* (Goldfuss); Desor in Agassiz & Desor, p. 123
1847 *Hemiaster parastatus* (Morton); Agassiz & Desor, p. 141
1847 *Hemiaster bufo* (Brongniart); Desor in Agassiz & Desor, p. 122
1847 *Hemiaster bucklandi* Desor in Agassiz & Desor, p. 123
1848 *Spatangus parastatus* Morton; Bronn, p. 1160
1852 *Holaster syriacus* Conrad in Lynch, p. 212; pl. 1: fig. 2
1853-60 *Hemiaster bucardium* (Goldfuss); d'Orbigny, p. 264; pl. 894: figs 1-5
1853-60 *Hemiaster bufo* (Brongniart); d'Orbigny, p. 217; pl. 873
1853-60 *Hemiaster globosus* (Agassiz); d'Orbigny, p. 260; pl. 892
1853-60 *Hemiaster minimus (*Agassiz*)*; d'Orbigny, p. 225; pl. 872
1853-60 *Hemiaster lacunosus* (Golfuss); d'Orbigny, p. 267, pl. 896

1853-60 *Hemiaster ricordeaui* d'Orbigny, p. 223; pl. 871

1853-60 *Hemiaster parastatus* (Morton); d'Orbigny, p. 265; pl. 894: fig. 4

1853-60 *Hemiaster parastatus* (Morton); d'Orbigny, p. 270

1853-60 *Hemiaster bucklandii* Desor; d'Orbigny, p. 231; pl. 893

1854 *Hemiaster desori* d'Archiac & Haime, p. 198; pl. 2: fig. 6

1854 *Hemiaster morrisi* Forbes in Morris, p. 81

1854 *Hemiaster asterias* Forbes in Morris, p. 81

1854 *Hemiaster baylei* Forbes in Morris, p. 81

1854 *Hemiaster toucasanus* d'Orbigny, p. 239; pl. 880

1857-69 *Hemiaster bufo* (Brongniart); Cotteau & Triger, p. 208; pl. 24: figs 8-9

1857-69 *Hemiaster cenomanensis* Cotteau & Triger, p. 210; pl. 34: figs 7-8

1857-69 *Hemiaster gracilis* Cotteau & Triger, p. 211; pl. 35: figs 9-12

1857-78 *Hemiaster griepenkerli* von Strombeck in Cotteau, p. 260: pl. 70

1857-78 *Hemiaster oriens* Cotteau, p. 72

1858 *Hemiaster parastatus* (Morton); Desor, p. 373

1858 *Hemiaster humphreysanus* Meek & Hayden, p. 147

1859 *Holaster parastatus* (Morton); Gabb, p. 19

1859 *Hemiaster humphreysanus* Meek & Hayden; Gabb, p. 19

1862 *Hemiaster desvauxi* Coquand, p. 247; pl. 26: figs 3-5

1864-82 *Epiaster loriolii* Wright, p. 265; pl. 59

1864-82 *Hemiaster morrisi* Forbes; Wright, p. 262; pl. 61

1864-82 *Hemiaster asterias* Forbes; Wright, p. 266; pl. 60: fig. 3

1864-82 *Hemiaster baylei* Forbes; Wright, p. 264; pl. 60: fig. 2

1873 *Hemiaster frontacutus* Stoliczka, p. 10; pl. 1: fig. 1

1873 *Hemiaster similaris* Stoliczka, p. 10; pl. 1: fig. 1

1875-91 *Hemiaster granosus* Coquand in Cotteau *et al.*, p. 111; pl. 4: figs 1-4

1875-91 *Hemiaster hippocastanum* Coquand in Cotteau *et al.*, p. 137; pl. 8: figs 9-12

1875-91 *Hemiaster proclivus* Peron & Gauthier in Cotteau *et al.*, p. 121; pl. 5: figs 1-4

1875-91 *Hemiaster setifensis* Peron & Gauthier in Cotteau *et al.*, p. 129; pl. 5: figs 5-7

1875-91 *Hemiaster zitelli* Coquand in Cotteau *et al.*, p. 136; pl. 8: figs 6-8

1875-91 *Hemiaster numidicus* Gauthier in Cotteau *et al.*, p. 76; pl. 7: figs 2-4

1881 *Hemiaster brahim* Peron & Gauthier in Cotteau *et al.*, p. 148; pl. 14: figs 6-9

1876 *Hemiaster humphreysanus* Meek & Hayden; Meek, p. 5: pl. 10: figs 1a-g

1877 *Hemiaster inkermanensis* de Loriol, p. 78; pl. 4: figs 5-7

1877 *Hemiaster orbignyanus* Lartet, p. 150; pl. 13: figs 11-12

1878 *Hemiaster gabrielis* Peron & Gauthier in Cotteau *et al.*, p. 116; pl. 13: figs 11-12

1880 *Hemiaster schlüteri* Coquand, p. 250

1881 *Hemiaster dewalquei* Cotteau, p. 30; pl. 2: figs. 7-9

1883 *Hemiaster difficilis* Bucaille, p. 21; pl. 4: figs 1-6

1883 *Hemiaster excavatus* Arnaud in Cotteau, p. 173; pl. 12: figs 1-4

1887 *Hemiaster wetherbyi* de Loriol, p. 391; pl. 17: figs 5-6

1887-8 *Hemiaster alcantarensis* de Loriol, p. 107; pl. 21: fig. 4

1887-8 *Hemiaster lusitanicus* de Loriol, p. 100; pl. 19: figs 1-7

1887-8 *Hemiaster palpebratus* de Loriol, p. 103; pl. 24: figs 1-3

1887-8 *Hemiaster subtilis* de Loriol, p. 106; pl. 21: figs 1-3

1887-8 *Hemiaster tumidosus* de Loriol, p. 102; pl. 19: figs 8-10

1889 *Hemiaster grossouvrei* Gauthier, p. 526; pl. 13: figs 1-3

1889 *Hemiaster rolandi* Gauthier, p. 17; pl. 1: figs 14-16

1891 *Hemiaster californicus* Clark, p. 77

1891 *Hemiaster humphreysanus* Meek & Hayden; Clark, p. 77

1891 *Hemiaster incrassatus* Clark, p. 77

1891 *Hemiaster parastatus* (Morton); Clark, p. 77

1891 *Hemiaster ungula* Clark, p. 77

1893 *Hemiaster humphreysanus* Meek & Hayden; Clark, p. 88; pl. 48: fig. 1

1893 *Hemiaster californicus* Clark; Clark, p. 90; pl. 49: figs 1a-c

1893 *Hemiaster humphreysanus* Meek & Hayden; Clark p. 52

1893 *Hemiaster parastatus* (Morton); Clark, p. 83; pl. 45: fig.1

1893 *Hemiaster ungula* Clark; Clark, p. 93; pl. 48: figs 3a-g

1894 *Hemiaster cossignyi* Lambert, p. 21; pl. 1: figs 20-22

1894 *Hemiaster icaunensis* Lambert, p. 73; pl. 2: fig. 18; text-figs 12-13.

1895 *Hemiaster longus* Cotteau & Gauthier, p. 40; pl. 6: figs 1-7

1895 *Hemiaster noemiae* Cotteau & Gauthier, p. 35; pl. 6: figs 1-7

1895 *Hemiaster opimus* Cotteau & Gauthier, p. 36; pl. 6: figs 8-11

1897 *Hemiaster tamulicus* Kossmat, p. 61, 96; pl. 10: fig. 5

1900 *Hemiaster blanckenhorni* Gauthier in Fourtau, p. 33; pl. 1: figs 11-12

1901 *Hemiaster burckhardti* Lambert; Burckhardt, p. 5; pl. 1: figs 1-4

1901 *Hemiaster* cf. *cristatus* Lambert; Burckhardt, p. 5; pl. 1: figs 5-8

1902 *Hemiaster noemiae* Cotteau & Gauthier var. *gulgulensis* Gauthier, p. 140; pl. 19; fig. 9

1903 *Hemiaster lamberti* Savin, p. 2; pl. 1: figs 12-18

1903a *Hemiaster sp.* Lambert, p. 87; pl. 3: figs 6-8

1905 *Hemiaster bufo* (Brongniart); Savin, p. 15

1906 *Hemiaster fanivelonensis* Lambert in Boule & Thevenin, p. 11; pl. 2: fig. 6

1906 *Hemiaster sp.* Lambert in Boule & Thévénin, p. 53; pl. 2: fig. 6

1907 *Hemiaster parastatus* (Morton); Weller, p. 298-300; pl. 15

1907 *Hemiaster kummeli* Clark in Weller, p. 302-3; pl. 17: figs 4-6

1907 *Hemiaster ungula* Clark; Weller, p. 301-2; pl. 16 figs 5-11

1907 *Hemiaster welleri* Clark in Weller, p. 302; pl. 17: figs 4-7

1907a *Hemiaster punctatus* var. *arizensis* Lambert, p. 721 (*nomen nudum*)

1907a *Hemiaster punctatus* var. *spissa* Lambert, p. 721 (*nomen nudum*)

1909 *Hemiaster lacunosus* (Goldfuss); Slocum, p. 10; pl. 2: figs 1-7

1909 *Hemiaster parastatus* (Morton); Slocum, p. 9-10

1910a *Hemiaster aragonensis* Lambert, p. 811; pl. 14; figs 6-7

1910a *Hemiaster incrassatus* Clark; Lambert, p. 813,; pl. 14: figs 11-12

1912 *Hemiaster* cf. *gabrielis* Peron & Gauthier; Fourtau, p. 62; pl. 6: fig. 7

1914 *Hemiaster balli* Fourtau, p. 65; pl. 5: fig. 6

1914 *Hemiaster gabrielis* Peron & Gauthier var. *aegyptiaca* Fourtau, p. 74; pl. 6: fig. 7

1915 *Hemiaster bexari* Clark in Clark & Twitchell, p. 89; pl. 46: fig. 1a-e

1915 *Hemiaster californicus* Clark; Clark & Twitchell, p. 96; pl. 50: fig. 1a-d

1915 *Hemiaster humphreysanus* Meek & Hayden; Clark in Clark & Twitchell, p. 95; pl. 49: fig. 2a-f

1915 *Hemiaster kummeli* Clark; Clark & Twitchell , p. 97; pl. 52: fig. 1a-c

1915 *Hemiaster lacunosus* (Goldfuss); Clark & Twitchell, p. 97; pl. 50: figs 3a-d; pl. 51: fig. 1a-i

1915 *Hemiaster parastatus* (Morton); Clark & Twitchell, p. 92; pl. 48: fig. 1a-n

1915 *Hemiaster ungula* Clark; Clark & Twitchell, p. 93; pl. 48: fig. 3

1915 *Hemiaster welleri* Clark; Clark & Twitchell, p. 98; pl. 52: fig. 2a-c

1916 *Hemiaster delawarensis* Clark, p. 751; pl. 47: figs 11-14

1916 *Hemiaster oriens* Cotteau; Lambert, p. 72

1917 *Hemiaster humphreysanus* Meek & Hayden; Dowling, p. 47; pl. 35: figs 1-1c

1918 *Hemiaster humphreysanus* Meek & Hayden; Ravn, p. 334; pl. 7: figs 1-2

1920 *Hemiaster alamedensis* Kew, p. 144; pl. 40: fig. 5

1920 *Hemiaster cholamensis* Kew, p. 146; pl. 41: fig. 1

1920 *Hemiaster oregonensis* Kew, p. 147; pl. 41: fig. 2

1920a *Hemiaster mancus* Lambert, p. 46; pl. 3: figs 14

1920a *Pusillaster dallonii* Lambert, p. 17; pl. 1: figs 20-21

1922 *Hemiaster berkoyi* Jackson, p. 73; pl. 12: fig. 10

1922 *Hemiaster dewalquei* Cotteau; Jackson, p. 73

1925 *Hemiaster rocaensis* Lambert in Lambert & Thiéry, p. 500

1925 *Hemiaster slocumi* Lambert in Lambert & Thiéry, p. 504

1925 *Hemiaster syriacus* (Conrad); Blanckenhorn, p. 103; pl. 8: figs 33-35

1927b *Hemiaster bexari* Clark; Lambert, p. 273

1928 *Hemiaster bexari* Clark; Adkins, p. 298

1930 *Hemiaster madagascariensis* forma A Cottreau; Besairie, p. 229; pl. 26: fig. 12

1930 *Hemiaster* sp. Besairie & Lambert, p. 110-111

1930 *Hemiaster zululandensis* Besairie & Lambert, p. 116; pl. 10: figs 3-4

1931 *Hemiaster barthouxi* Lambert, p. 196; pl. 5: figs 48-49

1931 *Hemiaster proclivus* Peron & Gauthier; Lambert, pl. 4: fig. 23

1931 *Hemiaster sourkoldjenouensis* Lambert, p. 146; pl. 4: figs 24-25

1932 *Hemiaster bufo* (Brongniart); Lambert, p. 115

1932 *Hemiaster granosus* Coquand; Lambert, p. 122

1932 *Hemiaster proclivus* Peron & Gauthier; Lambert, p. 144

1932 *Hemiaster saadensis* Peron & Gauthier; Lambert, p. 138

1932 *Hemiaster tumidosus* de Loriol; Lambert, p. 123

1933a *Distefanaster pygmeus* Lambert, p. 25; pl. 4: fig. 18

1933a *Hemiaster besairiei* Lambert, p. 22

1933a *Hemiaster mutabilis* Lambert, p. 20-21; pl. 3: figs 7-8

1933a *Hemiaster pseudoanticus* p. 21; pl. 2: figs 27-28

1933b *Hemiaster batalleri* Lambert, 187-188; pl. 1: figs 14-16

1935b *Hemiaster wetherbyi* de Loriol; Lambert, p. 372

1935c *Hemiaster tubillensis* Lambert, p. 519-520; pl. 57: figs 10-11

1936 *Hemiaster labriei* Lambert, p. 84-85; fig. 1; pl. 6: figs 5-7

1936 *Hemiaster madagascariensis* Cottreau var. *nana* Lambert, p. 205; pl. 24: figs 5-6

1936 *Hemiaster parallelus* Lambert, p. 206; pl. 24: figs 1-2

1936 *Hemiaster latesulcatus* Lambert, p. 206; pl. 24: figs 3-4

1937 *Hemiaster holoambitatus* Chiplonker, p. 64-65; pl. 6: figs 4a-c

1937 *Hemiaster stefaninii* Lang in Montanaro-Gallitelli & Lang, p. 204-205; pl. 9: fig. 12

1939 *Hemiaster balboi* Airaghi, p. 263; pl. 10: fig. 1

1941 *Hemiaster benhurensis* Stephenson, p. 67; pl. 7: figs 8-10

1941 *Hemiaster bexari* Clark; Stephenson, p. 65; pl. 6: figs 7-8; pl. 7: figs 5-7

1949 *Hemiaster (Integraster) dewalquei* Cotteau; Sánchez Roig, p. 239

1949 *Trachyaster antillensis* Sánchez Roig, p. 243

1953 *"Hemiaster" kümmeli* Clark; Cooke, p. 35; pl. 13: figs 5-6

1953 *Hemiaster arcolensis* Cooke, p. 32-33; pl. 12: figs 12-16

1953 *Hemiaster delawarensis* Clark; Cooke, p. 35; pl. 14: figs 6-9

1953 *Hemiaster humphreysanus* Meek & Hayden; Cooke, p. 30-31; pl. 12: figs 1-4

1953 *Hemiaster ungula* Clark; Cooke, p. 34-35; pl. 14: figs 10-14

1953 *Hemiaster welleri* Clark; Cooke, p. 35; pl. 14: figs 15-17

1953 *Hemiaster wetherbyi* de Loriol; Cooke, p. 31-32; pl. 12: 17-18

1955 *Hemiaster bufo* (Brongniart); Szörenyi, p. 123; pl. 22: figs 1-7, 11

1959 *Hemiaster parastatus* (Morton); Cooke, p. 67; pl. 28: figs 15-20

1962 *Hemiaster uwajimensis* Morishita, p. 114-115; pl. 1: figs 1-7

1967 *Hemiaster regulusanus* d'Orbigny; Devriès, p. 194; pl. 6: figs 42-44

1968 *Hemiaster uwajimensis* Morishita; Nisiyama, p. 196; pl. 18: figs 2,5,9

1984 *Hemiaster dewalquei* Cotteau; Kier, p. 19-20

1988 *Hemiaster (Hemiaster) bufo* (Brongniart); Smith *et al.*, p. 173; pl. 36: figs 1-4; text-figs 68, 69a, 70

1991 *Hemiaster proclivus* Peron & Gauthier; Smith & Bengtson, p. 53-54; pl. 11: figs d-f; text-fig. 43, 44, 45a-c

1991 *Hemiaster sp.* Smith & Bengtson, p. 54; pl. 11: figs g-j

1991 *Hemiaster syriacus* (Conrad); Néraudeau, p. 93

1993 *Hemiaster syriacus* (Conrad); Néraudeau *et al.*, p. 22, 294; pl. 4: figs f-g

1994 *Ditremaster pygmeus* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) alamedensis* Kew; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) antillensis* Sánchez Roig; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) batalleri* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) benhurensis* Stephenson; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) besairiei* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) bexari* Clark; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) cholamensis* Kew; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) delawarensis* Clark; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) excavatus* Arnaud; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) fanivelonensis* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) frontacutus* Stoliczka; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) globosus* (Agassiz); Néraudeau, table 2

1994 *Hemiaster (Bolbaster) gracilis* Cotteau & Triger; Néraudeau, table 1

1994 *Hemiaster (Bolbaster) holoambitus* Néraudeau, table 1

1994 *Hemiaster (Bolbaster) inkermanensis* de Loriol; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) labriei* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) latesulcatus* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) madagascariensis* Néraudeau, table 2

1994 *Hemiaster (Bolbaster) mutabilis* Lambert; Néraudeau, table 1

1994 *Hemiaster (Bolbaster) paralellus* Néraudeau, table 2

1994 *Hemiaster (Bolbaster) parastatus* (Morton); Néraudeau, table 2

1994 *Hemiaster (Bolbaster) similaris* Stoliczka; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) slocumi* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) sourkoldjenouensis* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) sp.* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) uwajimensis* Morishita; Néraudeau, table 1

1994 *Hemiaster (Bolbaster) wetherbyi* de Loriol; Néraudeau, table 2

1994 *Hemiaster (Hemiaster) alcantarensis* de Loriol; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) aragonensis* Néraudeau, table 1

1994 *Hemiaster (Hemiaster) asterias* Forbes; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) baylei* Forbes; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) bucklandii* Desor; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) bufo* (Brongniart); Néraudeau, table 1

1994 *Hemiaster (Hemiaster) cossignyi* Lambert; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) desori* d'Archiac & Haime; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) desvauxi* Coquand; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) difficilis* Bucaille; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) griepenkerli* von Strombeck; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) icaunensis* Lambert; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) incrassatus* Clark; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) lamberti* Savin; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) loriolii* Wright; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) lusitanicus* de Loriol; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) mancus* Lambert; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) minimus* (Agassiz); Néraudeau, table 1

1994 *Hemiaster (Hemiaster) morrisi* Forbes; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) noemiae* Cotteau & Gauthier; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) oriens* Cotteau; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) palpebratus* de Loriol; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) proclivus* Peron & Gauthier; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) ricordeaui* d'Orbigny; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) stefaninii* Lang; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) syriacus* (Conrad); Néraudeau, table 1

1994 *Hemiaster (Hemiaster) toucasi* d'Orbigny; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) tumidosus* de Loriol; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) zululandensis* Besairie & Lambert; Néraudeau, table 1

1994 *Hemiaster (Leymeriaster) pseudoanticus* Lambert; Néraudeau, table 1

1996 *Hemiaster (Bolbaster) madagascariensis* Cottreau; Greyling, p. 32; text-figs 8-10

2000 *Hemiaster madagascariensis* Cottreau; Smith & Jeffery, p. 326; text-fig. 134c

2000 *Hemiaster parastatus* (Morton); Smith & Jeffery, p. 326

2000 *Hemiaster* sp. indet. 1 Smith & Jeffery, p. 327

2000 *Hemiaster* sp. indet. 3 Smith & Jeffery, p. 327

2000 *Hemiaster* sp. indet. 4 Smith & Jeffery, p. 327-8

2000 *Hemiaster wetherbyi* de Loriol; Smith & Jeffery, p. 326-327

2007b *Hemiaster* sp. Gallemí *et al.*, p. 103

Genus **BOLBASTER** Pomel, 1869

[=*Leucaster* Gauthier in Peron, 1887, type species *L. remensis* Gauthier in Peron, 1887; =*Peroniaster* Gauthier, 1887, type species *P. cotteaui* Gauthier, 1887; =*Integraster* Lambert & Thiéry 1924, type species *Hemiaster ligeriensis* d'Orbigny, 1853]

TYPE SPECIES

Spatangus prunella Lamarck, 1816 by original designation.

DIAGNOSIS

Test globular to spherical; ovate in outline with no frontal notch and a vertically truncate posterior. Apical system central. Anterior ambulacrum narrow. Paired petals weakly sunken with anterior pair approximately twice as long as the posterior pair.

REMARKS

See discussion in the remarks on *Hemiaster* of how *Bolbaster* can be distinguished from *Hemiaster*. Detailed morphometric analysis is needed to establish the validity of the many nominal species listed by Néraudeau (1994). Here I divide the genus into two species groups.

***Bolbaster prunella* group**

This group is characterized by having narrow, parallel-sided petals.

1816 *Spatangus prunella* Lamarck, p. 33

1847 *Hemiaster nucula* Desor in Agassiz & Desor, p. 122; pl. 86

1847 *Hemiaster angustipneustes* Desor in Agassiz & Desor, 122

1850 *Hemiaster nasutulus* Sorignet, p. 53

1853-60 *Hemiaster prunella* (Lamarck) d'Orbigny, p. 242; pl. 881

1853-60 *Hemiaster nucula* Desor; d'Orbigny, p. 259; pl. 891

1853-60 *Hemiaster stella* (Morton); d'Orbigny, p. 245; pl. 882

1876 *Hemiaster nasutulus* Cotteau, p. 349; pl. 76: figs 5-6

1887 *Leucaster remensis* Gauthier in Peron, p. 213; pl. 7: figs 8-12

1887 *Peroniaster cotteaui* Gauthier in Peron, p. 390; pl. 7: figs 1-7

1910 *Hemiaster nucula* Desor; Lambert, p. 26; pl. 1: figs 24-26

1920b *Pusillaster dallonii* Lambert, p. 159; pl. 1: fig. 20-21

1925 *Peroniaster nasutulus* (Sorignet); Lambert & Thiéry, p. 507

1925 *Hemiaster remensis* (Gauthier); Lambert & Thiéry, p. 500

1978 *Peroniaster cotteaui* Gauthier; Kutscher, p. 1030; pl. 1

1988 *Hemiaster (Bolbaster) nasutulus* Sorignet; Smith *et al.*, p. 178; pl. 37: figs 1-4; pl. 38: figs 1-2; text-figs 68, 69b, 71

1994 *Hemiaster (Bolbaster) prunella* (Lamarck); Néraudeau, table 2

1994 *Hemiaster (Bolbaster) nucula* Desor; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) nasutulus* Sorignet; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) angustipneustes* Desor; Néraudeau, tables 1-2

1994 *Hemiaster (Bolbaster) remensis* (Gauthier); Néraudeau, table 2

1994 *Hemiaster (Bolbaster) cotteaui* (Gauthier) Néraudeau, table 2

2000 *Hemiaster prunella* (Lamarck); Smith & Jeffery, p. 320-322; text-fig. 134d-e

2000 *Hemiaster stella* (Morton); Smith & Jeffery, p. 223-224; text-fig. 134 a,b,f (part)

2000 *Hemiaster nucula* Desor; Smith & Jeffery, p. 322-323

***Bolbaster punctatus* group**

This group is characterized by having slightly wider, bowed petals.

1816 *Spatangus punctatus* Lamarck, p. 328

1830 *Spatangus stella* Morton, p. 245; pl. 3: fig. 11

1834 *Spatangus stella* Morton, p. 78; pl. 3: fig. 18

1847 *Hemiaster stella* (Morton); Agassiz & Desor, p. 141

1853-60 *Hemiaster punctatus* d'Orbigny, p. 250; pl. 886

1853-60 *Hemiaster ligeriensis* d'Orbigny, p. 255; pl. 887

1853-60 *Hemiaster koninckí* d'Orbigny, p. 250; pl. 885

1858 *Hemiaster stella* (Morton); Desor, p. 373

1859 *Hemiaster stella* (Morton); Gabb, p. 19

1871 *Hemiaster regulusanus* d'Orbigny; Geinintz, p. 15; pl. 5: fig. 2

1887 *Peroniaster gauthieri* Peron, p. 522; pl. 7: fig. 6

1893 *Hemiaster stella* (Morton); Clark, p. 84; pl. 44: fig. 1a-d

1896-99 *Hemiaster aquisgranensis* Schlüter, p. 123; pl. 10: figs 1-2

1889 *Hemiaster auberti* Thomas & Gauthier in Gauthier, p. 20; pl. 1: figs 17-18

1907 *Hemiaster stella* (Morton); Weller, p. 300-301; pl. 16: figs 1-4

1909 *Hemiaster neustriae* Lambert, p. 25; figs 20-23

1910 *Hemiaster dallonii* Lambert, p. 812; pl. 14: figs 8-10

1911 *Hemiaster rutoti* Lambert; Lambert, p. 52; pl. 3: figs 3, 5

1914 *Hemiaster* sp. indet. Checchia-Rispoli, p. 307; pl. 1: fig. 9

1915 *Hemiaster stella* (Morton); Clark & Twitchell, p. 93; pl. 48: fig. 2a-d

1920 *Hemiaster cottreaui* Lambert, p. 47; pl. 3: figs 12-13

1921 *Hemiaster Paronai* Checchia-Rispoli, p. 27-29; pl. 8: fig. 24;pl. 9: figs 14,18

1922 *Hemiaster madagascariensis* forma B Cottreau, p. 118; pl. 2: figs 4-5, 7-8

1925 *Hemiaster* (*Integraster*) *ligeriensis* Lambert & Thiéry, p. 504

1925 *Hemiaster* (*Leymeriaster*) *geinitzi* Lambert & Thiéry, p. 501

1933a *Hemiaster integer* Lambert, p. 21-22; pl. 3: figs 5-6

1933 *Linthia paronai* (Checchia-Rispoli); Checcia-Rispoli, p. 11; pl. 1: figs 5-7

1935b *Hemiaster sphericus* Lambert, p. 372-373; pl. 16: figs 18-19

1936 *Hemiaster heteropneustes* Lambert, p. 28; pl. 4: figs 20-22

1946 *Hemiaster cranium* Cooke, p. 226-227; pl. 32: figs 1-4

1953 *Hemiaster amelianus* Cooke, p. 35; pl. 16: fig. 1

1959 *Hemiaster* cf. *Hemiaster cranium* Cooke; Santos & Cuhna, p. 12; pl. 1: fig. 5; pl. 2: figs 1-6

1967 *Hemiaster punctatus* d'Orbigny; Devriès, p. 194; pl. 6: figs 34-41

1981 *Hemiaster cranium* Cooke; Brito, p. 402

1985 *Hemiaster aquisgranensis* Schlüter; van der Ham, p. 147; text-figs 1-4

1987 *Hemiaster aquisgranensis* Schlüter; van der Ham *et al.*, p. 33; pl. 20: fig. 1

1989 *Hemiaster (Bolbaster) hattaensis* Ali, p. 409; text-fig. 6 (5-8)

1992 *Hemiaster aquisgranensis* Schlüter; van der Ham & van Birgelen, p. 150; pl. 4: fig. 6

1994 *Hemiaster (Bolbaster) integer* Lambert; Néraudeau, table 1

1994 *Hemiaster (Hemiaster) dallonii* Lambert; Néraudeau, table 1

1994 *Hemiaster (Bolbaster) ligeriensis* d'Orbigny; Néraudeau, tables 1-2

1994 *Hemiaster (Bolbaster) punctatus* d'Orbigny; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) geinitzi* Lambert & Thiéry; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) hattaensis* Ali; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) paronai* Checchia-Rispoli; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) aquisgranensis* Schlüter; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) konincki* d'Orbigny; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) stella* (Morton); Néraudeau, table 2

1994 *Hemiaster (Bolbaster) amelianus* Cooke; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) neustriae* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) auberti* Gauthier & Thomas; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) rutoti* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) heteropneustes* Lambert; Néraudeau, table 2

1994 *Hemiaster (Bolbaster) cottreaui* Lambert; Néraudeau, p. Table 2

1995 *Hemiaster hattaensis* Ali; Smith, p. 232-233; pl. 32: figs 5-8; text-fig. 81

1995 *Hemiaster paronai* Checcia-Rispoli; Smith, p. 233, 236; pl. 33: figs 1-4; text-fig. 81

2000 *Hemiaster koninckanus* d'Orbigny; Smith & Jeffery, p. 322

2000 *Hemiaster hattaensis* Ali; Smith & Jeffery, p. 324

2000 *Hemiaster paronai* Checchia-Rispoli; Smith & Jeffery, p. 324; text-fig. 135a-c

2007a *Hemiaster* (*Bolbaster*) aff. *punctatus* Gallemí *et al.*, text-fig. 9g

2007b *Hemiaster* (*Bolbaster*) *punctatus* Gallemí *et al.*, text-fig. 10i-n

Genus **HOLANTHUS** Lambert & Thiéry, 1924

TYPE SPECIES

Holanthus hickmanni Koehler, 1914, by original designation (Recent of Atlantic and Pacific)

DIAGNOSIS

Test with approximately circular outline in oral view, and wedge-shaped in profile. Apical system ethmophract with four gonopores. Anterior ambulacrum narrow, sunken on upper surface but flush by the ambitus. Paired petals very broad with ambulacra strongly pinched as they cross the peripetalous fasciole. Peristome kidney-shaped. Sternal plates approximately symmetrical.

REMARKS

Smith (2005) emphasized the fact that *Holanthus* differs from other hemiasterids by having straight petals that are very broad, bowed paired petals with the ambulacra strongly pinched immediately below the terminations of the petals. *Proraster* also has pinched ambulacra, but is easily distinguished by its deep and broad anterior groove and strongly flexed anterior paired petals. Lambert & Thiéry (1924) included a number of Cretaceous forms with broad petals, but these lack the characteristic pinched ambulacra and are considered here to belong to the genus *Mecaster*.

Holanthus hawkinsi (Lambert, 1933a)

1908b *Hemiaster* (*Leucaster*) *lamberti* Cottreau, p. 173; pl. 5: fig. 3a; text-fig. 15

1922 *Hemiaster madagascarensis* forma A Cottreau, p. 118; pl. 2: figs 1-3, 6

1925 *Hemiaster* (*Bolbaster*) *hawkinsi* Lambert in Lambert & Thiéry, p. 505

1933a *Hemiaster hawkinsi* Lambert, p. 22; pl. 4: fig. 19

1979 *Hemiaster* (*Bolbaster*) *hawkinsi* Lambert; Tanaka *et al.*, p. 32; pl. 1: fig. 4; text-figs 5-8

?1979 *Hemiaster* (*Bolbaster*) cf. *madagascariensis* Cottreau; Tanaka *et al.*, p. 33; pl. 1: fig. 5

1996 *Hemiaster* (*Bolbaster*) sp. Parma, p. 231

2000 *Hemiaster stella* (Morton, 1830); Smith & Jeffery, p. 323 (part)

2005 *Hemiaster hawkinsi* Lambert; Parma & Casadío, p. 1080; text-figs 11-12

DIAGNOSIS

Apical system somewhat posterior of the midpoint. Paired petals narrower and more unequal in length than in other species of the genus.

OCCURRENCE

Maastrichtian and Danian of Madagascar (Tanaka *et al.* 1979; BMNH) and Argentina (Parma & Casadío 2005).

REMARKS

Holanthus hawkinsi strongly resembles *Bolbaster*, but it distinguished by having strongly pinched ambulacra below the terminations of the paired petals. This species is distinguished from Tertiary species of *Holanthus* by having narrower paired petals. Preservation quality has meant that it has not been possible to identify pinched ambulacra in all the specimens listed

above, but they are considered to be synonyms as they are otherwise indistinguishable from specimens with strongly pinched ambulacra.

Genus **HETEROLAMPAS** Cotteau, 1862

TYPE SPECIES

Heterolampas maresi Cotteau, 1862, by original designation.

DIAGNOSIS

Broad, low test with a weak anterior groove that is flush at the ambitus. Semi-ethmolytic apical system. Long, sub-equal paired petals that are virtually flush. Peripetalous fasciole present.

REMARKS

Mauritanaster differs only in having more sunken petals and there may well be a case for synonymising the two genera. However, both are retained here pending examination of the Tertiary type material of *Mauritanaster*.

Heterolampas maresi Cotteau, 1862

1862 *Heterolampas maresi* Cotteau, p. 72, 108; pl. 10: figs 7-11
1880 *Heterolampas maresi* Cottreau; Coquand, p. 397
1881 *Heterolampas maresi* Cotteau; Cotteau *et al.*, p. 151; pl. 15: figs 1-5
1883 *Heterolampas maresi* Cotteau; Pomel, p. 44

DIAGNOSIS

As for genus.

OCCURRENCE

Campanian of Algeria (Cotteau *et al.* 1883).

REMARKS

Differs from *Mauritanaster mirabilis* in having longer and broader paired petals.

Genus **LEIOSTOMASTER** Lambert, 1920a

[=*Vomeraster* Lambert, 1920b, type species = *Hemiaster verrucosus* Coquand, 1862]

TYPE SPECIES

Leiostomaster gentili Lambert, 1920a, by original designation.

DIAGNOSIS

Test circular in apical view and somewhat wedge-shaped with an oblique posterior face in lateral view. Interambulacral plates convex. Apical system central, ethmophract with four gonopores. Anterior ambulacrum narrow and deeply sunken with differentiated pore-pairs. Paired petals sharply defined, strongly bowed and often deeply sunken. Peristome pentagonal and downward facing. Sternal plates close to symmetrical. Characteristic pustular tuberculation. Peripetalous fasciole present.

REMARKS

Distinguished from other hemiasterids by characteristic convex plating and pustular tuberculation. Smith (2005) pointed out that specimens previously assigned to genus *Vomeraster* differ only in having narrower and more weakly sunken petals and suggested that *Vomeraster* represents male specimens of *Leiostomaster*. This position is supported by the fact that the genus is shown by crystallographic criteria to employ non-planktotrophic development (this thesis, Chapter 4) and so sexual dimorphism is not unexpected. I thus treat *Vomeraster* as a synonym of this genus.

***Leiostomaster* sp. or spp.**

Figure 2.4.1 B-C

1862 *Hemiaster verrucosus* Coquand, p. 327; pl. 35: figs 20-21

1888 *Hemiaster bigoneti* Cotteau, p. 116; pl. 14: figs 4-8

1892 *Hemiaster subverrucosus* Gauthier, p. 17; pl. 4: figs 1-3

?1910b *Hemiaster vomer* Lambert, p. 10; pl.1: figs 44-46

1920a *Leiostomaster gentili* Lambert, p. 21; pl. 1: figs 15-19

1920b *Leiostomaster gentili* Lambert; Lambert p. 138

1932 *Leiostomaster bigoneti* (Cotteau); Lambert, p. 112

1932 *Leiostomaster gentili* Lambert; Lambert, p. 77

1932 *Vomeraster subverrucosus* (Gauthier); Lambert, p. 113

1932 *Vomeraster verrucosus* (Coquand); Lambert, p. 113

?2000 *Hemiaster* (*Bolbaster*) *vomer* Lambert; Néraudeau *et al.*, p. 464; text-figs 3.9-3.13

REMARKS

The type specimens of *L. bigoneti* and *L. gentili* are very similar to one another, as are those of *V. verrucosus* and *V. subverrucosus*. It is thus possible that all specimens ascribed to *Leiostomaster* and to *Vomeraster* belong to a single species, with *Leiostomaster* specimens representing the males and *Vomeraster* the females. However, additional study of a larger number of specimens is necessary before this can be stated with confidence.

OCCURRENCE

?Campanian of North Africa and ?Antarctica. The occurrence of this genus has been recorded as "Upper Senonian". Smith (2005) has suggested that these specimens might be Campanian in age and this is assumed to be the case for the purposes of this thesis.

While Lambert (1910b) recorded the presence of the genus in Antarctica, Néraudeau *et al.* (2000) reported additional Antarctic material that they argued represented the same species and was better to assigned to *Bolbaster* than *Vomeraster*. However, I consider the specimens studied by Néraudeau *et al.* (2000) to be too poorly preserved to draw this conclusion with certainty. The original material described by Lambert (1910b) needs to be restudied and I exclude these specimens from the statistical analyses presented in later chapters pending such a re-examination.

Genus **LEYMERIASTER** Lambert & Thiéry, 1924

TYPE SPECIES

Hemiaster leymeriei Desor in Agassiz & Desor, 1847, by original designation.

DIAGNOSIS

Ethmophract or semi-ethmolytic apical system. Anterior ambulacrum sunken near the apical system, but virtually flush by the ambitus. Anterior paired petals at least three times as long as posterior paired petals. Trapezoidal peripetalous fasciole that is indented between the anterior and posterior paired petals.

REMARKS

Distinguished from other hemiasterids by its extremely short posterior paired petals.

KEY TO CRETACEOUS SPECIES

1. Test strongly polygonal. *L. sexangulatus.*
   Test with smoothly rounded outline. Go to 2.

2. Apical system at approximately 75% of test length from anterior margin. *L. micranthus.*

Apical system at 50-60% of test length from the anterior margin. Go to 3.

4. Anterior paired petals strongly flexed forwards. *L. madagascariensis*

Anterior petals straight or weakly bowed. Go to 4.

4. Test at least as broad as long; ridges running from between pore-pairs of anterior ambulacrum to interambularal margins. Go to 5.

Test longer than broad; no ridges from between pore-pairs to interambulacral margins. Go to 7.

5. Highest point anterior of the apical system. *L. eluvialis.*

Highest point posterior of apical system. Go to 6.

6. Broad, bowed petals, in which the width is almost 50% of the length. *L. maestrichtensis.*

Relatively narrow petals, in which the width is approximately 30% of the length. *L. moulinsanus.*

7. Relatively low form (test height 60-65% of test length). *L. nucleus.*

Relatively high form (test height 70-75% of test length). Go to 8.

8. Highest point near the top of the posterior truncation; peripetalous fasciole straight across the anterior portion of the test. *L. similis.*

Highest point on horizontal posterior keel; peripetalous fasciole convex across the anterior portion of the test. *L. leymeriei.*

Leymeriaster leymeriei (Desor in Agassiz & Desor, 1847)

1847 *Hemiaster leymeriei* Desor in Agassiz & Desor, p. 122

1853-60 *Hemiaster Leymeriei* Desor; d'Orbigny, p. 232; pl. 875

1889 *Hemiaster leymeriei* Desor; Gauthier, p. 532; pl. 13: fig. 10

1994 *Hemiaster (Leymeriaster) leymeriei* Desor; Néraudeau, table 1

1998 *Hemiiaster (Leymeriaster) leymeriei* Desor; Neraudeau *et al.*, p. 327 text-fig. 7

DIAGNOSIS

Test high and longer than broad with widest point anterior of mid-length; highest point on horizontal posterior keel. Apical system sub-central and ethmophract with four gonopores. Peripetalous fasciole convex around the anterior of the test.

OCCURRENCE

Cenomanian (Gauthier 1889), Turonian (Agassiz & Desor 1847) and Santonian (MNHN) of France.

REMARKS

This species is very similar to *H. similis*, but is distinguished by having its high point on a horizontal posterior keel, rather than very close to the posterior margin and by having a convex, rather than straight, peripetalous fasciole around the anterior portion of the test.

Leymeriaster eluvialis van der Ham, 1995

1995 *Hemiaster (Leymeriaster) eluvialis* van der Ham, p. 156; pls 1-3; text-figs 3-4

2000 *Leymeriaster eluvialis* van der Ham, 1995; Smith & Jeffery, p. 328-329

DIAGNOSIS

Test slightly broader than long with highest point anterior of the apical system. Anterior ambulacrum bordered by sharp keels. Broad anterior paired petals. Peripetalous fasciole concave across the anterior portion of the test.

OCCURRENCE

Maastrichtian of the Maastricht area, Netherlands and Belgium (van der Ham 1995).

REMARKS

Distinguished by having the anterior part of test bulging so that the highest point of the test lies anteriorly of the apical system.

Leymeriaster madagascariensis (Cottreau, 1922)

1903a *Hemiaster sp.* Lambert, p. 87; pl. 3: figs 6-8
1906 *Hemiaster sp.* Lambert in Boule & Thévénin, p. 53; pl. 2: fig. 6
1922 *Hemiaster madagascariensis* forma B Cottreau, p. 118; pl. 2: figs 4-5, 7-8
2000 *Hemiaster madagascariensis* Cottreau; Smith & Jeffery, p. 326; text-fig. 134c

DIAGNOSIS

Leymeriaster species with anterior paired petals strongly flexed forward, so as to run almost parallel to the anterior ambulacrum.

OCCURRENCE

Maastrichtian to Danian of south-west, north-west and east Madagascar (Lambert 1903a; Lambert in Boule & Thévénin 1906; Besairie 1971)

Leymeriaster maestrichtensis (Schlüter, 1897)

1897 *Hemiaster maestrichtensis* Schlüter, p. 32; pl. 2: figs 3-4

1955 *Hemiaster* (*Leymeriaster*) *maestrichtensis* Schlüter; Meijer, p. 74

1987 *Hemiaster maestrichtensis* (Schlüter); van der Ham *et al.*, p. 33; pl. 21: fig. 1

1994 *Hemiaster (Leymeriaster) maestrichtensis* Schlüter; Néraudeau, Table 2

1995 *Hemiaster* (*Leymeriaster*) *maestrichtensis* Schlüter; van der Ham, pl. 3: figs 6-10

1998 *Hemiaster* (*Leymeriaster*) *maestrichtensis* Schlüter; van der Ham & Jagt, fig. 1g

2000 *Leymeriaster maestrichtensis* (Schlüter); Smith & Jeffery, p. 328; text-fig. 136a-c

DIAGNOSIS

Test approximately as broad as long with high point immediately behind the apical system; no keels bordering the anterior ambulacrum. Raised interambulacral edges adjacent to the anterior ambulacrum with ridges extending from between the pore-pairs. Apical system slightly posterior and semi-ethmolytic. Peripetalous fasciole straight on anterior part of the test.

OCCURRENCE

Maastrichtian of the Maastricht area (van der Ham *et al.* 1987).

REMARKS

Differs from *L. eluvialis* in having the high point posterior of the apical system, no interambulacral keels adjacent to the anterior groove and a straight peripetalous fasciole on the anterior part of the test. Differs from *L. regulusi* by having broader petals. Differs from remaining *Leymeriaster* species in having a test with a smooth outline and a sub-central apical system.

Leymeriaster micranthus (Lambert, 1920a)

1920a *Hemiaster micranthus* Lambert, p. 48; pl. 2: figs 16-17

DIAGNOSIS

Short, wedge-shaped test with highest point at the top of the near vertical posterior truncation. Apical system situated at approximately 75% of total length from the anterior; plating unknown. Anterior ambulacrum very narrow.

OCCURRENCE

Santonian of Spain (Lambert 1920a; MNHN)

REMARKS

Distinguished from other species of *Leymeriaster* by the posterior position of the apical system.

Leymeriaster moulinsanus (d'Orbigny, 1851)

1853-60 *Hemiaster moulinsanus* d'Orbigny, p. 247; pl. 883
1853-60 *Hemiaster regulusanus* d'Orbigny, p. 248; pl. 884
?1871 *Hemiaster regulusanus* d'Orbigny; Geinintz, p. 15; pl. 5: fig. 2
?1925 *Hemiaster geinitzi* Lambert & Thiéry, p. 501
1925 *Hemiaster desmoulinsi* d'Orbigny; Lambert & Thiéry, p. 501
1925 *Hemiaster regulusi* d'Orbigny; Lambert & Thiéry, p. 501
1927a *Hemiaster regulusi* d'Orbigny; Lambert, p. 49
1936 *Hemiaster regulusi* d'Orbigny; Lambert, p. 83
?1984 *Hemiaster* (*Leymeriaster*) sp. aff. *regulusanus* d'Orbigny; Tanaka, p. 437; pl. 81: fig. 3; text-fig. 9.
1994 *Hemiaster (Leymeriaster) regulusi* d'Orbigny; Néraudeau, table 2

DIAGNOSIS

Test with smooth outline and highest point behind the apical system. Apical system subcentral, plating unknown. Anterior ambulacrum probably has ridges extending from between the pore-pairs to the interambulacral margins (see van der Ham 1995). Anterior paired petals approximately one third as wide as long.

OCCURRENCE

'Senonian' of France, Spain, Germany, Turkey and ?Japan (Néraudeau 1994).

REMARKS

Distinguished from *L. maestrichtensis* by having narrower anterior paired petals.

Leymeriaster nucleus (Desor in Agassiz & Desor, 1847)

1847 *Hemiaster nucleus* Desor in Agassiz & Desor, p. 122
1853-60 *Hemiaster nucleus* Desor; d'Orbigny, p. 240; pl. 876
?1885 *Hemiaster soulieri* Fallot, p. 258; pl. 8: figs 2-3
1935c *Hemiaster nucleus* Desor; Lambert, p. 519; pl. 57: fig. 12
1994 *Hemiaster (Leymeriaster) nucleus* Desor; Néraudeau, Table 1

DIAGNOSIS

Test with smooth outline and of moderate height; highest point on posterior keel running from the top of the posterior truncation and apical system. Apical system sub-central with four gonopores. Peripetalous fasciole almost straight across the anterior portion of the test.

OCCURRENCE

Turonian (Néraudeau 1994) and Santonian (Lambert 1935c) of France and Spain.

REMARKS

Leymeriaster nucleus is closest to *L. leymeriei* and *L. similis*, but is distinguished on the basis of having a considerably lower overall form.

Leymeriaster sexangulatus (d'Orbigny 1854)

1854 *Hemiaster sexangulatus* d'Orbigny, p. 256; pl. 889

1873 *Hemiaster sexangulatus* d'Orbigny; Stoliczka, p. 18; pl. 3: fig. 6

1897 *Hemiaster sexangulatus* d'Orbigny; Kossmat, p. 106

?1971 *Hemiaster aff. sexangulatus* d'Orbigny; Akkus, p. 16

?1984 *Hemiaster* (*Leymeriaster*) *polygonalis* Tanaka, p. 435; pl. 81: figs 1-2; text-figs 7-8

?1994 *Hemiaster (Leymeriaster) polygonalis* Tanaka; Néraudeau, Table 2

1994 *Hemiaster (Leymeriaster) sexangulatus* d'Orbigny; Néraudeau, Table 2

2000 *Leymeriaster sexangulatus* (d'Orbigny, 1854); Smith & Jeffery, p. 339-330

DIAGNOSIS

Strongly angular test with widest point at mid-length and highest point on strong posterior keel. Apical system slightly posterior and semi-ethmolytic. Peripetalous fasciole convex on the anterior part of the test.

OCCURRENCE

Campanian and Maastrichtian of India (Kossmat 1897), ?Maastrichtian of Turkey (Akkus 1971), and ?Campanian of Japan (Tanaka 1984).

REMARKS

Distinguished from other species of *Leymeriaster* by its strongly polygonal outline.

Leymeriaster similis (d'Orbigny, 1854)

1853-60 *Hemiaster similis* d'Orbigny, p. 229; pl. 874
1856 *Hemiaster Leymeriei* Hébert, p. 199
1889 *Hemiaster similis* d'Orbigny; Gauthier, p. 531; pl. 13: fig. 9
1994 *Hemiaster (Leymeriaster) similis* d'Orbigny; Néraudeau, Table 1

DIAGNOSIS
Test high and longer than broad with widest point anterior of mid-length; highest point close to the top of the steep posterior truncation. Apical system sub-central and ethmophract with four gonopores. Peripetalous fasciole straight around the anterior of the test.

OCCURRENCE
Cenomanian of France (Néraudeau 1994) and ?India (BMNH).

REMARKS
Closest to *L. leymeriei*, but distinguished by having its high point positioned more posteriorly and having a straight peripetalous fasciole on the anterior part of the test.

***Leymeriaster* spp. indet. (not seen)**

I have not been able to verify the following records of *Leymeriaster*:
1873 *Hemiaster vignesi* Lartet, p. 78; pl. 9: fig. 18
1911 *Hemiaster sancti-paterni* Lambert, p. 109
1857-69 *Hemiaster nucleus* Cotteau & Triger, pl. 52: figs 10-11
1994 *Hemiaster (Leymeriaster) sanctipaterni* Lambert; Néraudeau, table 2

1994 *Hemiaster (Leymeriaster) vignesi* Lartet; Néraudeau, table 1

Genus **MAURITANASTER** Lambert, 1920b

TYPE SPECIES

Mauritanaster gentili Lambert, 1920b by original designation (Palaeocene of Morocco and possibly Egypt).

DIAGNOSIS

Broad, low test with a weak anterior groove that is flush or weakly sunken at the ambitus. Semi-ethmolytic apical system. Long, sub-equal paired petals that are weakly sunken. Peripetalous fasciole present.

REMARKS

Heterolamapas differs only in having less sunken petals and there may well be a case for synonymising the two genera. However, both are retained here pending examination of the Tertiary type material of *Mauritanaster*.

Mauritanaster mirabilis (Peron & Gauthier in Cotteau *et al.*, 1881)

Figure 2.4.1 A

1881 *Hemiaster mirabilis* Peron & Gauthier in Cotteau *et al.*, p. 145; pl. 14: figs 1-5

1932 *Hemiaster mirabilis* Peron & Gauthier; Lambert, p. 130

2000 *Maurianaster mirabilis* (Peron & Gauthier); Smith & Jeffery, p. 348

DIAGNOSIS

Paired petals of moderate width that reach approximately four fifths of the distance to the ambitus.

OCCURRENCE

Maastrichtian of Algeria (Cotteau *et al.* 1881; Smith & Jeffery 2000).

REMARKS

This species is very similar to *H. maresi*, differing only in having slightly shorter and narrower petals. Differs from post-Cretaceous species of *Mauritanaster* in completely lacking a frontal notch.

Genus **MECASTER** Pomel, 1883

[=*Jordaniaster* Neumann, 1999, type species *J. husseini* Neumann, 1999]

TYPE SPECIES

Hemiaster fourneli Agassiz & Desor 1847, by original designation.

DIAGNOSIS

Low ovate to rectangular test. Apical system semi-ethmolytic or ethmolytic. Petals long and sub-equal in length. Complete peripetalous fasciole present.

REMARKS

The taxonomy of the genus *Mecaster* is currently in an unsatisfactory state: a large number of nominal species have been erected (for example, Lambert & Thiéry (1925) listed 86 species), but few are likely to represent distinct species. The problem is compounded by the fact that the marginal fascioles are variably developed in the genus, leading to many representatives being erroneously assigned to *Periaster*. Smith & Bengtson (1991) made important inroads into the problem by defining four species groups within the genus. This work is extended here by assigning, where possible, the species of *Mecaster* described in the literature to a species group. The four groups of Smith & Bengtson are:

Mecaster batnensis group

- Apical system central and semi-ethmolytic.
- Genital plate G4 in contact with madreporite and separates plate G2 from plate OV.
- Sternal suture meets labral plate close to its right hand edge.

Mecaster scutigera group

- Only this species.
- Distinctive apical system in which the madreporite separates the posterior genital plates but not the posterior ocular plates (i.e. semi-ethmolytic) and in which plate G4 is separated from the madreporite by plates G3 and OV.

Mecaster cubicus group

- Only this species.
- Semi-ethmolytic apical system.
- Extremely long labral plate.
- Peristome very close to anterior margin and opens forwards.

Mecaster fourneli group

- Fully ethmolytic apical system.
- Plate G4 is usually (but not always – see Smith & Bengtson, fig. 50e) separated from the madreporite by G3 and OV.
- Apical system wide so that gonopores open far from the midline; gonopores on the same side of the midline open close to one another.
- Sternal suture meets labral plate sub-centrally.

Thus, in this scheme, all *Mecaster* species bar *M. cubicus* and *M. scutigera* are assigned to either the *M. batnensis* or the *M. fourneli* group. Smith & Bengtson (1991) noted that, in addition to the differences noted above, the *M. fourneli* group can be further distinguished from the *M. batnensis* group by having (1) a slightly more elongate form; and (2) relatively more pores in

the anterior ambulacrum. They showed that, for South American specimens, pre-Turonian specimens assigned to *M. batnensis* could be distinguished from post-Turonian specimens assigned to *M. fourneli* using bivariate plots of these features against specimen length (Smith & Bengtson 1991, fig. 47).

In the present study an attempt was made to assign the many European and especially North African species to the groups of Smith & Bengtson (1991). In order to do this 64 specimens from the collections of the MNHN, Paris were studied and the following features were recorded:

- Age
- Locality
- Length
- Width
- Apical system plating
- Number of pore pairs in the anterior ambulacrum
- Nature of the sternal suture (straight vs. oblique).

When the specimen width and the number of pore pairs in the anterior ambulacrum were plotted against specimen length (Figure 2.4.2), neither plot was able to distinguish between either *M. batnensis* from *M. fourneli* or pre-Turonian from post-Turonian specimens. Thus, it was not possible to use these features in the classification of European and North African *Mecaster* specimens into species groups. This leaves only the plating of the apical disc and the obliquity of sternal suture as characters useful for distinguishing the two groups.

Here I assign the records of *Mecaster* in the literature to one of the species groups identified by Smith & Bengtson (1991), or to additional species groups identified here.

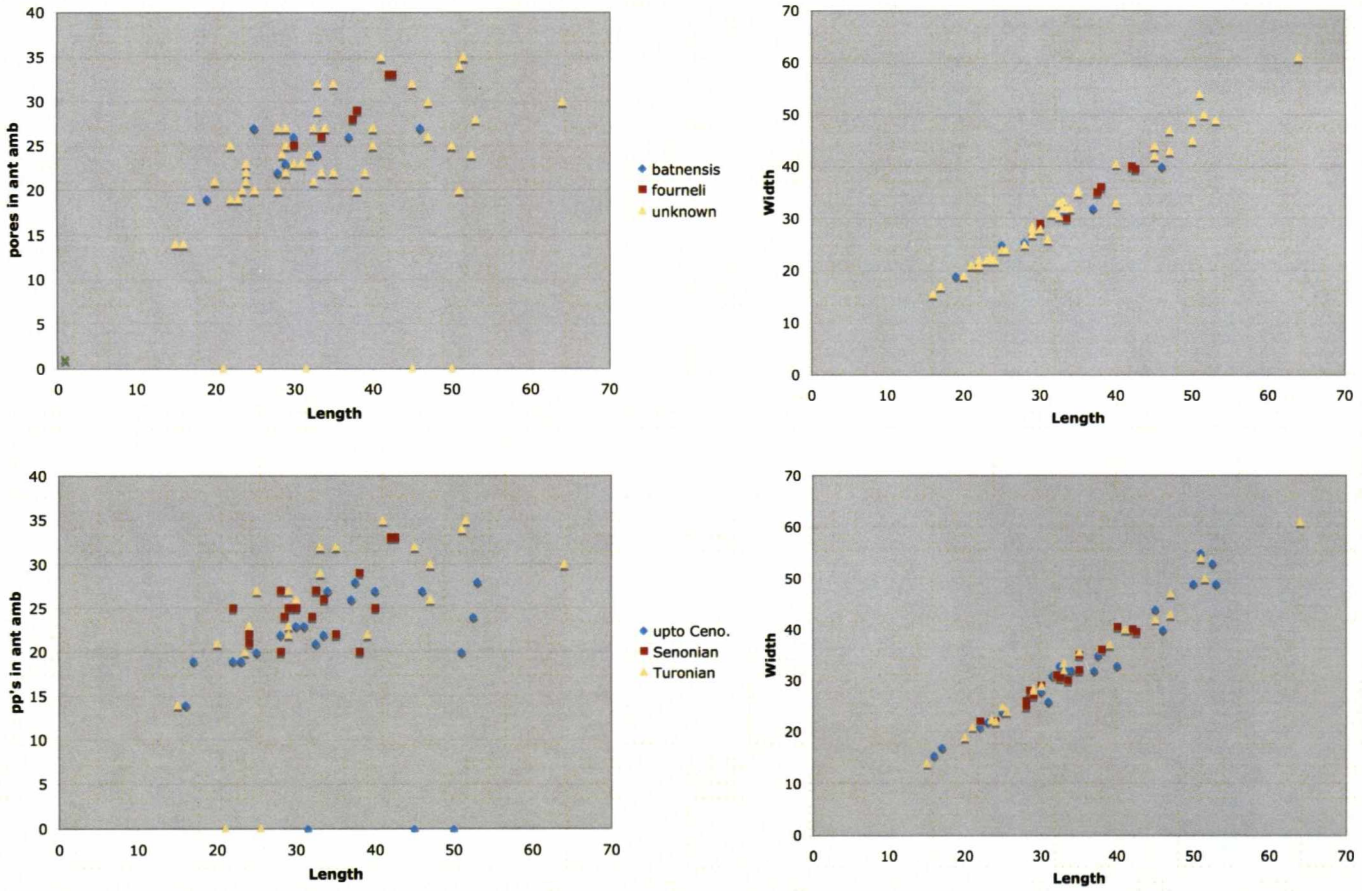

Figure 2.4.2: Graphs showing biometric comparisons of *Mecaster* specimens from North Africa. The relationships between the number of pore-pairs in the anterior ambulacrum (left hand side) and test width (right hand side) and test length are examined in specimens of different species (top) and of different ages (bottom).

Mecaster batnenisis group

Figure 2.4.1 F-G, I

This group is characterized by:

1. Apical system central and semi-ethmolytic
2. Genital plate G4 in contact with madreporite and separates G2 from OV.
3. Sternal suture meets labral plate close to its right hand edge.

1862 *Hemiaster batnensis* Coquand, p. 248; pl. 26: figs 6-8

1862 *Hemiaster heberti* Coquand, p. 242; pl. 25: figs 7-9

1875-91 *Hemiaster batnensis* Coquand; Cotteau *et al.*, p. 118

1875-91 *Hemiaster heberti* Coquand; Cotteau *et al.*, p. 129; pl. 7: figs 1-3

1875-91 *Hemiaster latigrunda* Peron & Gauthier; Cotteau *et al.*, p. 69; pl. 5: figs 1-5

1875-91 *Hemiaster pseudo fourneli* Peron & Gauthier in Cotteau *et al.*, p. 113; pl. 4: figs 5-8

1875-91 *Hemiaster asperatus* Peron & Gauthier in Cotteau *et al.*, p. 66; pl. 1: figs 4-7

1875-91 *Hemiaster bibansensis* Peron & Gauthier in Cotteau *et al.*, p. 68; pl. 3: figs 6-7

1875-91 *Hemiaster meslei* Peron & Gauthier in Cotteau *et al.*, p. 102; pl. 2: figs 5-8

1875-91 *Hemiaster ameliae* Peron & Gauthier in Cotteau *et al.*, p. 109; pl. 3: figs 7-11

1875-91 *Hemiaster chauveneti* Peron & Gauthier in Cotteau *et al.*, p. 135; pl. 8: figs 1-5

1875-91 *Hemiaster auressensis* Peron & Gauthier in Cotteau *et al.*, p. 62; pl. 3: figs 1-3

1875-91 *Hemiaster krenchalensis* Peron & Gauthier in Cotteau *et al.*, p. 64; pl. 4: figs 1-4

1875-91 *Hemiaster ksabensis* Peron & Gauthier; Cotteau *et al.*, p. 70; pl. 3: figs 1-5

1875-91 *Hemiaster semicavatus* Peron & Gauthier in Cotteau *et al.*, p. 71; pl. 4: figs 5-8

1875-91 *Hemiaster thomasi* Peron & Gauthier in Cotteau *et al.*, p. 72; pl. 3: fig. 8; pl. 4: fig. 1

1875-91 *Hemiaster jullieni* Peron & Gauthier in Cotteau *et al.*, p. 124; pl. 5: figs 8-11

1875-91 *Hemiaster gabrielis* Peron & Gauthier in Cotteau *et al.*, p. 166; pl. 4: figs 9-12

1880 *Hemiaster superbissimus* Coquand, p. 204

1880 *Hemiaster tenouklensis* Coquand, p. 241

1880 *Micraster laforeti* Coquand, p. 250

1880 *Hemiaster expulsus* Coquand, p. 239

1880 *Hemiaster krenchelensis* Peron & Gauthier; Cortazar, p. 64; pl. 4: figs 1-4

1880 *Hemiaster nemrod* Coquand, p. 240

1880 *Hemiaster guillieri* Coquand, p. 266

1885 *Hemiaster batnensis* Coquand; Gauthier, p. 259; pl. 7: fig. 1

1885 *Hemiaster latigrunda* Peron & Gauthier; Gauthier, p. 260; pl. 7: fig. 5

1887-8 *Hemiaster delgadoi* de Loriol, p. 104; pl. 20: figs 4-8

1887-8 *Hemiaster bellacensis* de Loriol, p. 108; pl. 21: figs 5-8

1895 *Hemiaster iranicus* Cotteau & Gauthier, p. 33; pl. 5: figs 7-12

1902 *Hemiaster devolutus* Gauthier, p. 117; pl. 17: figs 13-14

1902 *Hemiaster parthicus* Gauthier, p. 137; pl. 20: figs 1-2

1902 *Hemiaster figarii* Gauthier in Fourtau, p. 25; pl. 2: figs 16-17

1914 *Hemiaster pseudofourneli* Peron & Gauthier; Fourtau, p. 82, 109

1914 *Hemiaster cunninghami* Fourtau, p. 48; pl. 5: figs 7-8

1914 *Hemiaster gabrielis* Peron & Gauthier var. *aegyptica* Fourtau, p. 74; pl. 6: fig. 7

1921 *Hemiaster gabrielis* Peron & Gauthier var. *aegyptica* Fourtau, p. 87

1921 *Hemiaster hassani* Fourtau, p. 88; pl. 11: figs 13-14

1921 *Hemiaster jullieni* Peron & Gauthier; Fourtau, p. 91

1921 *Hemiaster heberti* Coquand var. *turonensis* Fourtau, p. 89; pl. 11

1925 *Hemiaster jacksoni* Maury, p. 518-521

1933 *Hemiaster semicavatus* Peron & Gauthier; Lambert, p. 74

1935a *Hemiaster bibasensis* Peron & Gauthier; Lambert, p. 361

1935a *Hemiaster guillieri* Coquand; Lambert, p. 363

1935a *Hemiaster schluteri* Coquand; Lambert, p. 361; pl. 16: figs 1-2

1937 *Hemiaster jacksoni* Maury; Maury, p. 279

1937 *Hemiaster cedroensis* Maury, p. 280-283; pl. 2: figs 3,7

?1938 *Hemiaster schoelleri* Lambert, p. 277-278; pl. 19: figs 1-3

1953 *Hemiaster jacksoni* Maury; Cooke, p. 33; pl. 12: figs 5-11

1959 *Hemiaster jacksoni* Maury; Santos & Cunha, p. 11; pl. 1: figs 1-4

1960 *Hemiaster saulcyanus* d'Orbigny; Devriès, p. 258; pl. 890: figs 1-8

1981 *Hemiaster cedroensis* Maury; Brito, p. 405; pl. 2: fig. 7

1985 *Hemiaster waynensis* Larrain, p. 1402; text-figs 1-3.

1991 *Mecaster batnensis* (Coquand) Smith & Bengtson, p. 56-60; pl. 12: figs a-l; pl. 13: figs a-n; text-figs 45d-g, 46, 47, 48a, 49

1991 *Mecaster semicavatus (*Peron & Gauthier*)* Néraudeau, p. 93

1991 *Mecaster pseudofourneli* (Peron & Gauthier); Néraudeau, p. 93

?1991 *Mecaster ameliae* (Peron & Gauthier); Néraudeau, p. 95

?1993 *Mecaster ameliae* (Peron & Gauthier); Néraudeau *et al.*, p. 23-4, 295; pl. 4: figs i-j

1993 *Mecaster batnensis* (Coquand); Néraudeau *et al.*, p. 22-3, 294; pl. 4: fig. h

1993 *Mecaster semicavatus* (Peron & Gauthier); Néraudeau *et al.*, p. 25-6, 297; pl. 4: figs m-o

1993 *Mecaster pseudofourneli* (Peron & Gauthier); Néraudeau *et al.*, p. 24-5, 296; pl. 4: figs k-l

1995 *Mecaster pseudofourneli* (Peron & Gauthier); Néraudeau *et al.*, p. 418-419; text-figs 6d-e, 7.

1995 *Mecaster orbignyanus* (Desor, 1857); Néraudeau *et al.*, p. 419-420; text-figs 6c, 8

1997 *Mecaster pseudofourneli* (Peron & Gauthier) Néraudeau & Courville, p. 840-842; text-figs 6.3, 6.7

1997 *Mecaster* cf. *pseudofourneli* (Peron & Gauthier); Néraudeau & Courville, p. 842; text-fig. 6.9

1998 *Mecaster batnensis* (Coquand); Neraudeau *et al.*, p. 328; text-fig. 7

***Mecaster cubicus* group**

Figure 2.4.1 D-E, H

This group is characterized by:

1. Semi-ethmolytic apical system.
2. Peristome very close to the anterior margin and opens forwards
3. Extremely long labral plate.

1847 *Hemiaster cubicus* Desor in Agassiz & Desor, p. 124

1853-60 *Hemiaster cubicus* Desor; d'Orbigny, p. 237; pl. 879

1903 *Hemiaster cubicus excentricus* Fourtau, p. 179; text-fig. 2

1914 *Hemiaster cubicus* Desor; Fourtau, p. 67; pl. 6: figs 1-5

1921 *Hemiaster cubicus* Desor; Fourtau, p. 87

1925 *Hemiaster cubicus* Desor; Blanckenhorn, p. 99; pl. 8: figs 28-29

1990 *Hemiaster cubicus* Desor; Smith *et al.*, p. 64; text-figs 19e-h, 21

***Mecaster scutiger* group**

This group is characterized by:

1. Distinctive apical system in which the madreporite separates the posterior genital plates but not the posterior ocular plates (i.e. semi-ethmolytic) and in which plate G4 is separated from the madreporite by plates G3 and OV.

1850 *Brissus scutiger* Forbes in Sharpe, p. 198: pl. 25: fig. 5

1887-8 *Brissus scutiger* Forbes; de Loriol, p. 98; pl. 18: figs 4, 12

1914 *Hemiaster proximus* Fourtau, p. 82; pl. 8: fig. 2

1932 *Hemiaster scutiger* (Forbes); Lambert, p. 126

?1997 *Mecaster aff. scutiger* (Forbes); Néraudeau & Courville, p. 842; text-fig. 6.10

***Mecaster africanus* group**

This group is characterized by:

1. Inflated test with a strongly oblique posterior.
2. Semi-ethmolytic apical system.
3. Anterior paired petals almost reach the ambitus.

1862 *Hemiaster africanus* Coquand, p. 247; pl. 25: figs 10-12

1875-91 *Hemiaster brossardi* Cotteau *et al.*, p. 127; pl. 11: figs 2-5

1875-91 *Hemiaster obliquetruncatus* Cotteau *et al.*, p. 60; pl. 2: figs 1-4

1875-91 *Hemiaster lorioli* Peron & Gauthier in Cotteau *et al.*, p. 127; pl. 6: figs 5-8

1875-91 *Hemiaster saadensis* Peron & Gauthier in Cotteau *et al.*, p. 125; pl. 6- figs 1-4

1875-91 *Hemiaster bouruignati* coquand in Cotteau *et al.*, p. 128; pl. 6: figs 9-10

1879 *Hemiaster africanus* Coquand; Cotteau *et al.*, p. 58

1880 *Hemiaster athenais* Coquand; Coquand, p. 245

1887 *Hemiaster africanus* Coquand; Gauthier, p. 412; text-fig. 10-11

1925 *Hemiaster percevali* Lambert & Thiéry, p. 502

1932 *Hemiaster africanus* Coquand; Lambert, p. 138

1983 *Hemiaster jacksoni* Maury; Bidar in Bengtson, p. 44-45 (part)

1991 *Mecaster africanus* (Coquand); Smith & Bengtson, p. 62-64; pl. 16: figs a-d; text-fig. 51

***Mecaster victoris* group**

This group is characterized by:

1. Fully ethmolytic apical system.
2. Narrow, shallow, parallel-sided petals.

1854 *Hemiaster verneuili* d'Orbigny, p. 235; pl. 878: fig. 1-9

1875-91 *Linthia durandi* Peron & Gauthier in Cotteau *et al.*, p. 75; pl. 4: figs 6-9; pl. 5: fig 1

1880 *Hemiaster ararensis* Coquand, p. 267

1883 *Hemiaster arnaudi* Cotteau, p. 172; pl. 11: figs 6-8

1889 *Periaster fischeri* Gauthier, p. 22, pl. 4: figs. 30-33

1905 *Linthia duncani* Fourtau, p. 162, pl. 3: figs. 1, 4

1931 *Hemiaster verneuili* d'Orbigny var. *revestensis* Lambert, p. 135

1932 *Hemiaster victoris* Lambert, p. 127; pl. 4: figs 18-19

1932 *Periaster fischeri* Gauthier; Lambert, 132, pl. 8: figs. 5-7

1935a *Hemiaster victoris* Lambert; Lambert, p. 363

1939 *Periaster subsexangulatus* Airaghi, p. 264; pl. 10: figs 2-3

1960 *Hemiaster arnaudi* Cotteau; Devriès, p. 75; pl. 3: fig. 8-10

1989 *Periaster subsexangulatus* Airaghi; Ali, p. 410; text-fig. 5(8)

1995 *Mecaster victoris* (Lambert); Smith, p. 236; pl 34: figs 4-7; text-figs 82-84

2000 *Mecaster victoris* (Lambert); Smith & Jeffery, p. 330

***Mecaster nicaisei* group**

This group is characterized by:

1. Very broad paired petals. This group resembles the genus *Holanthus*, but differs in lacking the characteristic pinched ambulacra exhibited by *Holanthus*.

1862 *Hemiaster nicaisei* Coquand, p. 326; pl. 35: figs 22-23
1862 *Hemiaster aumalensis* Coquand, p. 249; pl. 26: figs 9-11
1880 *Hemiaster fowleri* Coquand, p. 248
1880 *Hemiaster procumbens* Coquand, p. 240
1902 *Hemiaster kanapanensis* Gauthier, p. 133; pl. 19: figs 5-6
1914 *Hemiaster latistella* Fourtau, p. 78; pl. 7: fig. 3
1932 *Hemiaster solignaci* Lambert, p. 118; pl. 4: figs 13-14
1932 *Hemiaster verneuili* d'Orbigny var. *bedoulensis* Lambert, p. 135

***Mecaster fourneli* group**

Figure 2.4.1 J

This group is characterized by:
1. Fully ethmolytic apical system.
2. Plate G4 is usually (but not always – see Smith & Bengtson (1991) fig. 50e) separated from the madreporite by G3 and OV.
3. Apical system wide so that gonopores open far from the midline; gonopores on the same side of the midline open close to one another.
4. Sternal suture meets labral plate sub-centrally.

1847 *Hemiaster fourneli* Deshayes in Agassiz & Desor, p. 17
1875-91 *Hemiaster messai* Peron & Gauthier in Cotteau *et al.*, p. 64; pl. 4: figs 2-5
1880 *Hemiaster campichei* Coquand, p. 244
1880 *Hemiaster consobrinus* Peron & Gauthier in Cotteau *et al.*, p. 66; pl. 3: figs 6-10

1880 *Hemiaster distractus* Coquand, p. 258

1881 *Hemiaster fourneli* Deshayes; Cotteau *et al.*, p. 58, 132, 149; pl. 2: figs 1-8

1889 *Periaster charmesi* Thomas & Gauthier in Gauthier, p. 23; pl. 1: figs. 21-23

1902 *Hemiaster morgani* Gauthier, p. 131; pl. 19: figs 3-4

1905 *Hemiaster alyi* Fourtau, p. 166; pl. 3: fig. 2

1914 *Hemiaster Sanfilippoi* Checchia Rispoli, p. 306; pl. 1: fig. 10

1915 *Hemiaster texanus* Clark in Clark & Twitchell, p. 94; pl. 49: figs 1a-j

1928 *Hemiaster teilhardi* Basse, p. 115-116; figs 3-4; pl. 7: figs 1a-b

1933 *Hemiaster fourneli* Deshayes; Checchia-Rispoli, p. 10; pl. 1: fig. 8

1939 *Hemiaster messai* Peron & Gauthier; Airaghi, p. 262; pl 10: figs 4-5

1939 *Periaster zinai* Airaghi, p. 265; pl. 10: fig. 6

1983 *Hemiaster messai* Peron & Gauthier; Roman & Sornay, p. 13; pl. 1: figs 2-4

1991 *Mecaster fourneli* (Deshayes); Smith & Bengtson, p. 61-62; pl. 14: figs a-m; pl. 15: figs a-l; pl. 16: figs e-f; text-figs 45k-l, 47, 48b, 50.

1997 *Mecaster aff. fourneli* (Deshayes); Néraudeau & Courville, p. 842-844; text-fig. 6.12

2000 *Mecaster fourneli* Deshayes; Smith & Jeffery, p. 330; text-fig. 135 d-f.

***Mecaster* sp. indet.**

These following list of specimens includes those that are too poorly preserved to be assigned to one of the above groups, as well as those which I have not seen as part of this study and are either too poorly figured to be assigned to a group or in references that I have not been able to obtain.

1853-60 *Hemiaster saulcyanus* d'Orbigny, p. 258; pl. 890

1873 *Hemiaster luynesi* Cotteau; Lartet, p. 76; pl. 9: figs 15-17

1887-8 *Hemiaster adonessensis* de Loriol, p. 110; pl. 22: figs 1-2

1880 *Hemiaster limpidus* Coquand, p. 245

1880 *Hemiaster barroisi* Coquand, p. 263

1884-1905 *Hemiaster ibelensis* de Loriol, p. 30; pl. 7: fig. 7

1884-1905 *Hemiaster kfourensis* de Loriol, p. 32; pl. 8: figs 2-6

1885 *Hemiaster baroni* Fallot, p. 256; pl. 8: fig. 1

1895 *Hemiaster decussatus* Cotteau & Gauthier, p. 12; pl. 1: fig. 8

1897 *Hemiaster pullus* Kossmat, p. 95; pl. 10: fig. 6

1905 *Hemiaster toxasteristoma* Fourtau, p. 33; pl. 4: figs 1-14

1905 *Hemiaster humei* Fourtau, p. 167; pl. 3: fig. 3

1914 *Hemiaster newtoni* Fourtau, p. 79; pl. 7: figs 4-5

1914 *Hemiaster sineus* Fourtau, p. 86; pl. 8: fig. 4

1915 *Hemiaster beecheri* Clark & Twitchell, p. 96; pl. 50: fig. 2a-c

1919 *Hemiaster mianii* Stefanini, p. 152; pl. 5: fig. 11

1925 *Hemiaster italicus* Lambert in Lambert & Thiéry, p. 502

1925 *Hemiaster lambesensis*, Gauthier (manuscript) in Lambert & Thiéry, p. 502

1925 *Hemiaster kossmati* Lambert & Thiéry, p. 503

1925 *Hemiaster gumbeli* Coquand (manuscript) in Lambert & Thiéry, p. 503

1939 *Hemiaster (Mecaster) chirakhanensis* Chiplonker, p. 240-241; pl. 25: figs 4a-b

1953 *Hemiaster beecheri* Clark; Cooke, p. 31

1959 *Hemiaster oliveirai* Santos & Cunha, p. 13-15; pl. 3: figs 1-4

1981 *Linthia oliveirai (*Santos & Cuhna); Brito, p. 574; pl. 3: figs 7-9

1997 *Mecaster* sp. A Néraudeau & Courville, p. 844; text-fig. 6.2

Genus **PALHEMIASTER** Lambert, 1916

TYPE SPECIES

Palhemiaster peroni Lambert, 1916, by original designation.

DIAGNOSIS

Apical system sub-central and semi-ethmolytic. Sunken, sub-equal paired petals. Oblique sternal suture. Peripetalous fasciole only developed on the posterior part of the test.

REMARKS

This genus resembles the *Mecaster batnensis* group, but differs from this and all other hemiasterids in having a peripetalous fasciole that is only developed on the posterior part of the test. The toxasterid *Pliotoxaster* is also similar in appearance, but differs from *Palhemiaster* in that it completely lacks a peripetalous fasciole.

Palhemiaster peroni Lambert, 1916

1916 *Palhemiaster peroni* Lambert, p. 71
1920b *Palhemiaster peroni* Lambert; Lambert, p. 160; pl. 2: figs 1-5
1932 *Palhemiaster peroni* Lambert; Lambert, p. 43, 68

DIAGNOSIS

Test globular with a rounded, rather than truncate, posterior; test does not taper strongly to the posterior. Paired petals long; anterior pair practically reaching the ambitus. Peristome approximately 33% of test length from the anterior margin. Anus clearly visible when viewed from above.

OCCURRENCE

Aptian and Albian of Algeria (Lambert 1920b, 1932).

REMARKS

Differs from *P. calvini* and *P. ibericus* in having longer anterior paired petals, a less anterior peristome and having a test that is rounded, rather than truncate, at the posterior. Differs additionally form *P. ibericus* in having a less tapered test.

Palhemiaster calvini (Clark, 1893)

1893 *Hemiaster calvini* Clark, p. 90-91; pl. 49: fig. 2a-i
1915 *Hemiaster calvini* Clark; Clark in Clark & Twitchell, p. 91: pl. 47: fig. 2a-i
1927b *Epiaster calvini* (Clark); Lambert, p. 272
?1927b *Hemiaster comanchei* Clark; Scott
?1932 *Palhemiaster scotti* Lambert, p. 112

DIAGNOSIS
Test globular with a strong posterior keel and steeply truncate posterior face; test does not taper strongly to the posterior. Anterior paired petals reaching approximately 85% of the distance to the ambitus; posterior petals equal in length to anterior pair. Peristome approximately 20-25% of test length from the anterior margin.

OCCURRENCE
Albian to Cenomanian of Texas (Clark & Twitchell 1915).

REMARKS
Differs from *P. peroni* in having shorter petals and a more anterior peristome and a truncate posterior face. Differs from *P. ibericus* in having a steeper posterior face, a stronger posterior keel and relatively longer posterior petals.

Palhemiaster scotti was erected by Lambert (1932) for a specimen figured by Scott (1927) in a thesis. It has not been possible to study this specimen, but the brief description given by Jeannet (1935) suggests it may belong to *P. calvini.*

Palhemiaster ibericus Jeannet, 1935

1934 *Palhemiaster ibericus* Jeannet, p. 388 (*nomen nudum*)

1935 *Palhemiaster ibericus* Jeannet; Jeannet, p. 181; pl. 1: figs 1-3; text-figs 1-2

DIAGNOSIS

Test low with an obliquely truncate posterior face; it lacks a strong posterior keel and tapers to the posterior. Anterior paired petals reaching approximately 85% of the distance to the ambitus; posterior petals approximately 85% of the length of the anterior pair. Peristome approximately 20-25% of test length from the anterior margin.

OCCURRENCE

Aptian of Ibiza, Balearic Islands (Jeannet 1934, 1935).

REMARKS

Differs from *P. peroni* and *P.calvini* in having a lower test that tapers to the posterior and having unequal paired petals. Differs additionally from *P. peroni* in having shorter anterior paired petals and from *P.calvini* in having no pronounced posterior keel.

Genus ***PRORASTER*** Lambert, 1895

[=*Sanfilippaster* Checchia-Rispoli 1932, type species *S. geayi* Cottreau, 1908b, p. 26]

TYPE SPECIES

Schizaster atavus Arnaud, 1883 by original designation.

DIAGNOSIS

Test with deep, wide anterior groove with steep or overhanging walls on apical surface. Anterior petals long strongly flexuous; posterior petals short and straight. Ambulacra strongly pinched below the ends of the petals.

Apical system ethmolytic or semi-ethmolytic with four gonopores, positioned posterior of centre. Labral plate short. Peripetalous fasciole only.

REMARKS

This genus has been placed in the family Schizasteridae by several recent authors e.g. Kier (1972), Smith (1995) and Smith & Jeffery (2000). On the other hand, Smith (2005) has considered *Proraster* to be a hemiasterid on the basis that it does not have an ethmolytic apical system (Smith personal communication 22.09.2006). While this is indeed true for *P. granti* (the species figured by Smith), which has a semi-ethmolytic apical disc, it is not the case for some other *Proraster* species, including the type species, which have a fully ethmolytic apical system. Nevertheless, the genus level phylogeny presented in the following chapter of this thesis supports the inclusion of *Proraster* within the hemiasterids.

Proraster atavus (Arnaud, 1883)

1883 *Schizaster atavus* Arnaud, p. 223, pl. 12: figs 5-9
1893 *Hemiaster dalli* Clark, p. 89, pl. 48: fig. 2
1895 *Opissater centrosus* Cotteau & Gauthier, p. 45, pl. 7: figs 10-15
1915 *Hemiaster dalli* Clark; Clark, in Clark & Twitchell, p. 90, pl. 47: fig. 1
1923 *Hemiaster* sp. (or spp.) indet. Hawkins, p. 206 (part)
1924 *Hemiaster* sp. indet. Hawkins, p. 316, pl. 18: fig. 3
1927a *Proraster atavus* (Arnaud); Lambert, p. 50, pl. 3: fig. 23
1934 *Hemiaster siboneyensis* Weisbord, p. 201, pl. 22: figs 7-9
1941 *Hemiaster dalli* Clark; Stephenson, p. 63, pl. 6: figs: 1-4
1949 *Hemiaster siboneyensis* Weisbord; Sánchez Roig, p. 237
1953 *Proraster dalli* (Clark); Cooke, p. 36, pl. 15: figs 1-5
1984 *Hemiaster siboneyensis* Weisbord; Kier, p. 17, pl. 8: figs 5-7
?1993 *Hemiaster* sp. or spp. Donovan, p. 101, fig. 12
?1993 *Hemiaster* sp. Donovan & Lewis, p. 187

2000 *Proraster atavus* (Arnaud); Smith & Jeffery, p. 340-341.

DIAGNOSIS

Test almost as broad as long; highest immediately behind the apical system. Broad anterior groove with sharp keels. Apical system ethmolytic with four gonopores. Anterior petals flexed and twice the length of the posterior petals, both pairs diverge at approximately 90°. Apical system at 50-55% of the test length from the anterior.

OCCURRENCE

Late Cretaceous of Cuba (Kier 1984); Senonian of France (Arnaud 1883); Upper Senonian (Campanian or Maastrichtian) of Iran (Cotteau & Gauthier 1895); Early Maastrichtian of Spain (Lambert 1927a) and ?Jamaica (Donovan 1993; Donovan & Lewis 1993); mid-Late Maastrichtian of Texas, USA (Cooke 1953). Also reported from the Palaeocene of Argentina (Parma & Casadío 2005).

REMARKS

Cooke differentiated *P. dalli* from *P. atavus* because the former has the gonopores on each side close together but far from those on the other side, whereas the latter has four equally spaced gonopores. In addition the madreporite extends further beyond the end of the posterior oculars in *P. dalli*. However, I consider these differences to be slight and follow Smith & Jeffery (2000) in treating the two species as synonyms.

Proraster geayi Cottreau, 1908b

1908b *Proraster geayi* Cottreau, p. 170, pl. 4: fig. 5; text-fig. 13
1922b *Proraster geayi* Cottreau; Cottreau p. 117, pl. 2: fig. 9
1932 *Sanfilippaster geayi* (Cottreau); Checchia-Rispoli p. 313, pl. 1

1994 *Proraster magnus* Markov, p. 66, pl. 3: fig. 1; text-fig. 18
1995 *Proraster geayi* Cottreau; Smith, p. 238; pl. 34: figs 1-3, 8
2000 *Proraster geayi* Cottreau; Smith & Jeffery, p. 342; text-fig. 140a-c

DIAGNOSIS
Test low, broader than long. Anterior ambulacrum very deeply sunken with overhanging keels that converge anteriorly. Apical system ethmolytic with four gonopores; positioned at approximately 60% of test length from the anterior. Anterior petals strongly flexed forwards so as to run subparallel to the anterior groove, they are approximately three times as long as the posterior petals. Posterior petals diverge at 120-160°. Peristome inclined forwards, opening into the frontal groove. Broad peripetalous fasciole.

OCCURRENCE
Maastrichtian of eastern Madagascar (Besairie 1971 MNHN) and southern India (BMNH); mid Maastrichtian of Oman (Smith 1995); mid-Late Maastrichtian of Libya (Checchia-Rispoli 1932).

REMARKS
Distinguished from *P. granti* by its longer posterior paired petals. Smith & Jeffery (2000) tentatively considered *P. morgani* and *Neoproraster usalrensis* to be juveniles of *P. geayi*, but they are considered as a separate species here (see below).

Proraster granti Kier, 1972

1972 *Proraster granti* Kier, p. 84-87; pl. 47: figs 6-7; pl. 48; text-fig. 45

DIAGNOSIS
Test low with overhanging posterior truncation. Anterior ambulacrum in deep groove. Apical system semi-ethmolytic with four gonopores; positioned

at 60-65% of test length from the anterior margin. Posterior paired petals approximately one fifth of the length of the anteriors; diverging at 150-170°.

OCCURRENCE

Campanian of Saudi Arabia (Kier 1972).

REMARKS

Similar to *P. geayi* but distinguished by having extremely short posterior petals, an anterior ambulacrum without convergent keels and an overhanging posterior truncation.

Proraster herrerae (Lambert & Sánchez Roig, in Sánchez Roig, 1926)

1926 *Opissaster herrerae* Lambert & Sánchez Roig, in Sánchez Roig p. 126, pl. 40: figs 1-2; pl. 41: fig. 3

1949 *Opissaster herrerae* Lambert & Sánchez Roig; Sánchez Roig, p. 244

1953 *Hemiaster gonzalezmunozi* Sánchez Roig, p. 170, pl. 11: figs 1-3

1984 *Hemiaster*? (*Trachyaster*) *gonzalezmunozi* Sanchez Roig; Kier, p. 18, pl. 7: figs 1-3

1984 *Hemiaster*? (*Trachyaster*) *herrerae* (Lambert & Sánchez Roig); Kier, p. 18, pl. 7: figs 4-8; pl. 8: fig. 1

2000 *Proraster herrerae* (Lambert & Sánchez Roig); Smith & Jeffery, p. 341-342.

DIAGNOSIS

Test broad, with anterior ambulacrum in a broad, sharply bounded groove that extends to the peristome. Apical system situated at 50-55% of test length from the anterior margin; ethmolytic with four gonopores. Anterior paired petals flexuous and approximately 1.5 times longer than the posterior pair; both pairs diverge at approximately 90°.

OCCURRENCE

Late Cretaceous of Cuba (Kier 1984), Maastrichtian of Jamaica (BMNH).

REMARKS

Differs from *P. atavus* in having a deeper frontal notch and proportionally longer posterior petals.

Proraster morgani (Cotteau & Gauthier, 1895)

1895 *Opissater morgani* Cotteau & Gauthier, p. 43, pl. 7: figs 6-9
1994 *Neoproraster usalrensis* Markov, p. 83, pl. 4: fig. 2; text-fig. 24

DIAGNOSIS

Small specimens with a broad anterior groove. Apical system at approximately 60% of the test length from the anterior margin; semi-ethmolytic with four gonopores. Anterior paired petals flexed forward, diverging at approximately 80°; posterior petals diverge at approximately 150° and are approximately one third of the length of the anterior pair.

OCCURRENCE

Campanian-Maastrichtian of Iran (Cotteau & Gauthier 1895); Late Maastrichtian of Kazakhstan (Markov 1994).

REMARKS

Smith & Jeffery (2000) tentatively considered the small taxa *P. morgani* and *Neoproraster usalrensis* to be juveniles of *P. geayi* that exhibited the flexed anterior petals and widely divergent posterior petals characteristic of this species, but were yet to develop the overhanging anterior keels. However, the anterior paired petals are also wider than in *P. geayi* and are more similar to those of *P. atavus* than *P. geayi*, so, in the absence of convincing

ontogenetic series, these specimens are provisionally retained as a separate species here.

2.5 FAMILY MICRASTERIDAE

Family **MICRASTERIDAE** Lambert, 1920b

DIAGNOSIS

Ethmophract or semi-ethmolytic apical system. Mesamphisternous plastron. Characteristic tuberculation with small tubercles set in a fine, uniform groundmass. Subanal fasciole present in most taxa, but may be secondarily lost.

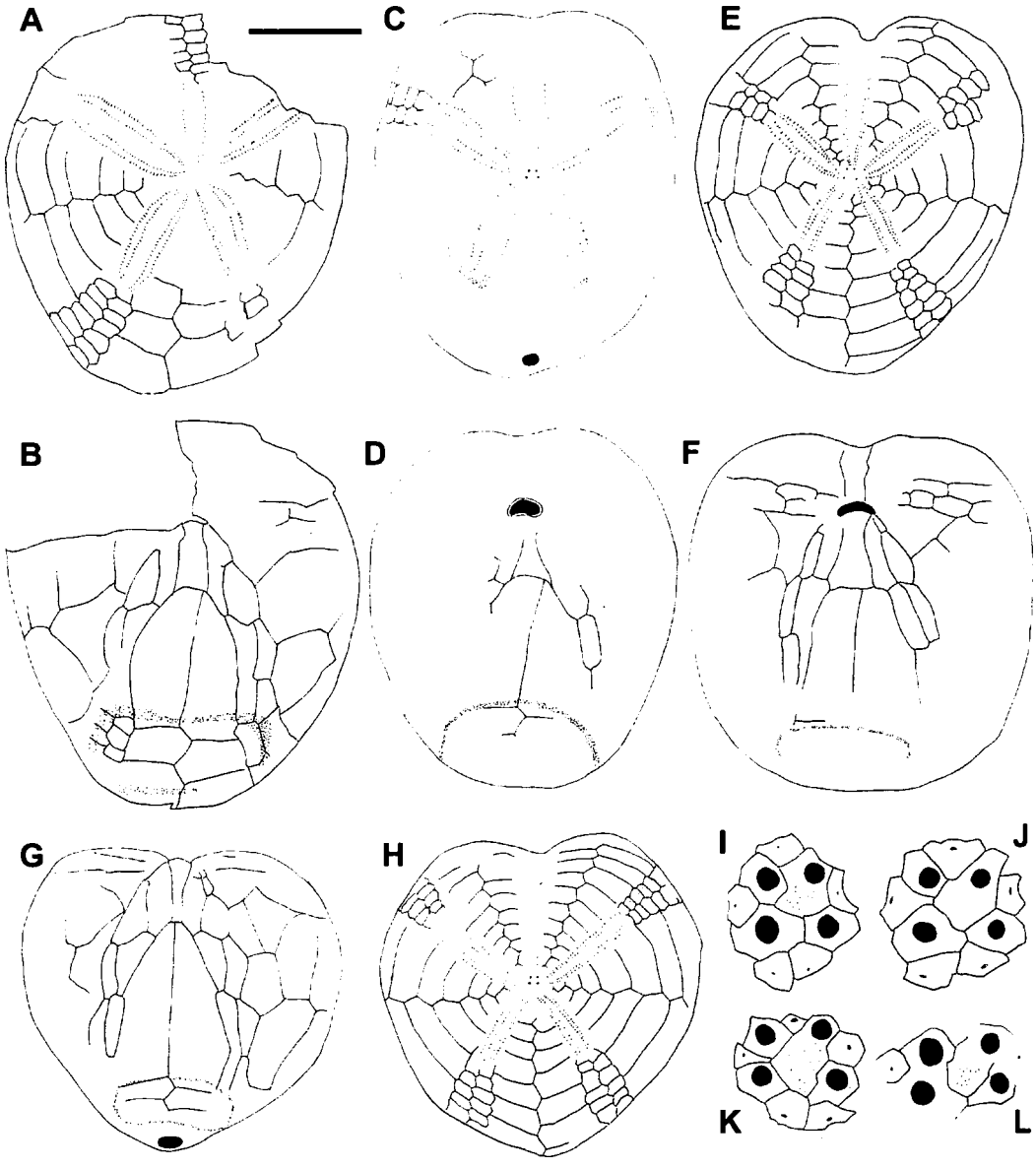

Figure 2.5.1: Micrasteridae. (**A-B**) *Plesiaster peini* BMNH EE8514, Campanian Upper Abiad Limestone of Jebel Herzeg, Tunisia, apical and oral views; (**C-D, L**) *Diplodetus americanus* USNM 76285, holotype, Maastrichtian Corsicana Marl of 6 miles east of Castroville, Texas, apical and oral views and apical system; (**E, J**) *Micraster schroederi* BMNH E75821, Lower Campanian of Holtwick, Westphalia, apical view; (**F, K**) *Micraster turonensis* BMNH E40977, 'Senonian' of France, oral view and apical sysyem; (**G-I**) *Micraster coranguinum* BMNH E32820 Santonian, locality unknown, oral and apical views and apical system. Relative scale bar: (A) 30.9 (B) 30.9 (C) 9.5 mm (D) 9.5 mm (E) 12.9 mm (F) 14.8 mm (G) 18.5 mm (H) 18.5 mm (I) 2.9 mm (J) 3.7 mm (K) 3.2 mm (L) 1.5 mm.

REMARKS

The micrasterids have been traditionally defined on the presence of a subanal fasciole. However, Smith & Jeffery (2000) noted that some taxa lack this feature while conforming to the family diagnosis in all other respects. Smith & Jeffery (2000) therefore suggest that the characteristic micrasterid tuberculation should be the primary characteristic used to place taxa in this family.

KEY TO CRETACEOUS GENERA

1. Three gonopores in apical system (plate G2 imperforate). Go to 2.
   Four gonopores in apical system. Go to 3.

2. Subanal fasciole present; pore-pairs in anterior ambulacrum differentiated; frontal groove cuts ambitus weakly. *Cyclaster.*
   No fascioles; pore-pairs of anterior ambulacrum similar to those in paired ambulacra; frontal groove does not cut ambitus. *Isaster.*

3. Paired ambulacra flush and apetaloid to subpetaloid. Go to 4.
   Paired ambulacra sunken and petaloid. Go to 5.

4. Peristome less than 10% of test length from the anterior margin. *Turanglaster.*
   Peristome at least 15% of test length from the anterior margin. *Ovulaster.*

5. Anterior ambulacrum similar to paired ambulacra. *Gibbaster.*
   Anterior ambulacrum apetaloid to subpetaloid. Go to 6.

6. Peristome less than 15% of test length from anterior margin and hidden by labral projection. *Micraster.*

Peristome greater than 15% of test length from anterior margin with opening clearly visible in oral view. Go to 7.

7. Paired petals broad with anteriors extending over 80% and posteriors over 60% of the distance to the ambitus. *Plesiaster.*

Narrow paired petals with anteriors extending less than 60% and posteriors less than 40% of the distance to the ambitus. *Diplodetus.*

Genus ***MICRASTER*** Agassiz, 1836

[=*Paramicraster* Maczynska, 1968, type species *Micraster coranguinum* var. *latior* Rowe, 1899]

TYPE SPECIES

Spatangus coranguinum Leske, 1778, by original designation.

DIAGNOSIS

Cordate test with distinct anterior groove. Apical system ethmophract with four gonopores. Anterior ambulacrum apetaoid to subpetaloid; paired ambulacra petaloid. Peristome less than 15% of test length from the anterior margin and covered by a prominent labral projection. Subanal fasciole usually present.

REMARKS

The morphological change in the genus *Micraster* through the Upper Cretaceous Chalk of Europe has been considered as one of the best examples of an evolutionary series in the fossil record of invertebrates and is cited in a number of textbooks (e.g. Benton & Harper 1997; Clarkson 1998). Rowe (1899) carried out what has become a classic work that documented the morphological changes in *Micraster* in the Chalk of England. Rowe's (1899) study has subsequently been extended and refined by a number of

workers (e.g. Kermack 1954; Maczynska 1968; Ernst 1970, 1972; Stokes 1975, 1977, 1979; Fouray 1981; David & Fouray 1984; Smith 1984; Olszewska-Nejbert 2007).

Despite the evolution of *Micraster* remaining a textbook classic, the taxonomy of the genus remains in a somewhat unsatisfactory state. There are three main reasons for this, which are outlined below.

Firstly, there are very few characters that have been used to distinguish very many species. The 100+ species of *Micraster* that have been named in the literature have been defined almost exclusively on the following four characters: 1. test shape; 2. position of the mouth; 3. prominence of the labral projection; and 4. sharpness of the groove between the two rows of pore-pairs in the paired petals. As a result many of the species in the literature are distinguished only on subtle differences in one or two of these characters, most typically test shape and position of the peristome. Furthermore, the large number of taxa in comparison to morphological characters makes cladistic analysis of the species of *Micraster* impractical (if not impossible).

Secondly, the taxonomic scheme used by British workers has diverged from that followed in continental Europe. The taxonomy of the genus was studied by Lambert (1895) who produced a comprehensive (but unillustrated) monograph covering all *Micraster* species then described. However, Rowe (1899) was "unable to consult" Lambert's monograph when completing his study of *Micraster* in the English chalk (Stokes 1977, p. 805). Subsequently, British workers have tended to follow the nomenclature used by Rowe (1899), while Lambert's (1895) scheme has been adhered to in continental Europe.

Thirdly, convergent evolution seems to have been prevalent within *Micraster*, opening up the possibility that very similar species have been derived from different ancestors. This is reflected in the phylogenetic schemes produced in the past, which sometimes imply polyphyletic origins of some species. For example, Stokes' (1975) diagram of *Micraster* phylogeny suggests that *M. coranguinum* is derived from *M. bucaillei* in the Northern Province, but from *M. decipiens* in the Anglo-Parisian Basin (figure 28 of Stokes 1975). Presumably Stokes was unable to distinguish *M. coranguinum* of the Northern Province from *M. coranguinum* of the Anglo-Parisian Basin on the basis of morphology.

Previous taxonomic schemes for the genus *Micraster* have frequently taken into consideration the geographical and stratigraphic distribution of fossil taxa (e.g. Ernst 1970, 1972; Stokes 1975). This has led to difficulties in naming taxa, such as the example of *M. coranguinum* discussed in the previous paragraph. However, an argument could be made that these careful studies incorporating geographical and stratigraphic information are the best way to study taxa like *Micraster* that have such an abundant fossil record and such a paucity of morphological characters. Pearson (e.g. 2001) has argued that stratophenetics (e.g. Gingerich 1990), rather than cladistics, is optimal in cases where sampling is dense and there is good stratigraphical continuity between samples. Pearson suggests that these conditions do not apply for 99% of the fossil record, but argues that they do in the case of planktonic foraminifera. Perhaps the genus *Micraster* may also represent another such case, though there is no objective way of making such a decision (and the somewhat sporadic sediment accumulation on the shelf in general, and in the Chalk in particular should be taken into consideration (Gale 2005)).

In my view, the optimum approach for studying the evolution of *Micraster* probably lies in the combination of both detailed stratigraphic and

morphological studies, such as those carried out by Ernst (1970, 1972), with morphometric analyses to determine the validity of species (e.g. David & Fouray 1984). In any event, it seems foolhardy to disregard the stratigraphic and geographical data that has been carefully gathered by previous workers (e.g. Rowe 1899; Ernst 1970; Stokes 1975).

A thorough revision of the entire genus *Micraster* along these lines represents a monumental task and one beyond the scope of this thesis. Instead I attempt to carry out a first step in such a process by placing species into groups based on morphology. In doing so, I have tried to be as sensitive as possible to the previous schemes based on stratigraphy and geography. I have also attempted to provide a comprehensive synonymy list in order to provide a useful resource to future workers attempting to revise the genus.

***Micraster coranguinum* group**

Figure 2.5.1 G, I

This group is characterized by:
1. Test approximately as broad as long.
2. A sharp groove running down the midline of the paired petals.
3. Peristome positioned at around 1/8 of test length from the anterior margin.
4. Labrum projecting strongly so that the mouth barely visible from below.
5. Periproct at approximately 2/3 of total test height from the base.
6. Periplastronal areas coarsely granulose.

1676 *Encephaloides* Plott, p. 92; pl. 2: fig. 11; pl. 7: fig. 9
1678 *Echinus praeter radios* Lister, p. 224; pl. 7: fig. 28
1699 *Echinites cordatus vulgaris* Luidii, p. 47; pl. 12: fig. 964
1734 *Micraster cor anguinum (α) anglicum* Klein, p. 100; pl. 12: fig. E

1778 *Spatangus cor anguinum (α) anglicum* Klein; Leske, p. 221, pl. 23: figs C-D

1778 *Spatangus cor anguinum (β) norvagicum* Klein; Leske, p. 225; pl. 23: figs A-B (part)

1791 *Spatangus cor anguinum* Leske; Brugières, pl. 155: figs 4-5

1811 *Spatangus cormaricum* Parkinson, p. 28, pl. 3: fig. 11

1822 *Spatangus rostratus* Mantell, p. 192; pl. 17: figs 10-17

1829 *Spatangus coranguinum* (Leske); Goldfuss, p. 157; pl. 48: fig. 6

1836 *Micraster cor-anguinum* (Leske); Agassiz, p. 184

1836 *Ananchytes coravium* Grateloup, p. 167; pl. 2: fig. 12

1847 *Micraster cor-anguinum* (Leske); Agassiz & Desor, p. 23 (part)

1850a *Micraster cor-anguinum* (Leske); Forbes, pl. 10: figs 1-7 (part)

1857-78 *Micraster coranguinum* (Leske); Cotteau, pl. 85: figs 4-5

1858 *Micraster cor-anguinum* (Leske); Desor, p. 207 (part)

1863 *Micraster sub-carinatus* Cotteau, p. 217

1869 *Micrater cor-anguinum* (Leske); Cotteau & Triger, p. 326, pl. 25: figs 5-10

1874 *Spatangus (Micraster) coranguinum* (Leske); Quenstedt, p. 644, pl. 87: figs 28, 33

1875 *Micraster cor-anguinum* (Leske); Loven, pl. 33

1878 *Micraster coranguinum* (Leske); Cotteau, p. 501; pl. 83: figs 4-5

1878 *Micraster cor-anguinum* (Leske); Wright, p. 271; pl. 32

1883 *Micraster rostratus* (Mantell); Bucaille, p. 34, pl. 8

1883 *Micraster regularis* Arnaud in Cotteau, p. 165; pl. 11: figs 1-5

1887 *Micraster cor anguinum* (Leske); Gauthier, p. 232

1892 *Micraster bucaillei* Parent, p. 15; pl. 1: fig. 1a-c

1895 *Micraster coranguinum* (Leske); Lambert, p. 163

1895 *Micraster merceyi* Munier Chalmas in Lambert, p. 165

1895 *Micraster rostratus* (Mantell); Lambert, p. 173

1895 *Micraster regularis* Arnaud; Lambert, p. 224

1895 *Micraster bucaillei* Parent; Lambert, p. 234

1899 *Micraster cor-anguinum* (Leske); Rowe, p. 538

1901 *Micraster coranguinum* (Leske); Lambert in Grossouvre, p. 961

1902 *Micraster cor testudinarium* Goldfuss; Wollemann, p. 31

1902 *Micraster cor anguinum* (Leske); Wollemann, p. 31 (part)

1907 *Micraster coranguinum* (Leske); Valette, p. 138

1907 *Micraster rostratus* (Mantell); Valette, p. 180

1911 *Micraster coranguinum* (Leske); Lambert, p. 7

1924 *Micraster coranguinum* (Leske); Chatwin, pl. 2: figs 4-5, 10

1942 *Micraster praecursor* Rowe; Wright & Wright, p. 119

1950 *Micraster* cf. *coranguinum* Saint-Seine, p. 310; text-fig. 1

1954 *Micraster coranguinum* (Leske); Kermack, pl. 24: fig. 12; pl. 25: fig. 14; pl. 26: fig. 16

1959 *Micraster coranguinum* Leske; Mosvkin & Poslavskaya, p. 281-282; pl. 20: figs 2 a-e; text-fig. 94

1959 *Micraster rostratus* (Mantell); Mosvkin & Poslavskaya, p. 282; pl. 21: figs 1 a-e; text-fig. 95

1964 *Micraster coranguinum* (Leske); Dzabarov, p. 55; pl. 18: ?fig. 2

1966 *Micraster coranguinum* (Leske); Ernst, p. 124

1966 *Micraster coranguinum* (Leske); Fischer, p. U581; text-fig. 467.2

1968 *Micraster coranguinum* (Leske); Pasternak *et al.*, p. 221, pl. 20: figs 1-4; text-fig. 49

1969 *Micraster coranguinum* (Leske); Cayeux, p. 37; pl. 1: figs 5-9

1974 *Micraster coranguinum* (Leske); Ernst & Schulz, p. 30; pl. 1: fig. 3; pl. 2: fig. 2; text-figs 7, 8b-c, 9d-e

1974 *Micraster coranguinum* (Leske); Savchinskaya, p. 328; pl. 113: figs 7-10

1975 *Micraster coranguinum* (Leske); Stokes, p. 64, pl. 2: figs 1-3, text-figs 24c, 29d

1975 *Micraster coranguinum simpsoni* Stokes, p. 65; pl. 3: figs 1-5; text-fig. 29f

1975 *Micraster coranguinum rostratus* (Mantell); Stokes, p. 65; pl. 2: figs 4-7; text-fig. 29e

1975 *Micraster bucaillei* Parent; Stokes, p. 63

1975 *Micraster westlakei* Stokes, p. 81, pl. 12: figs 4-6; text-fig. 30h

1975 *Micraster regularis* Arnaud; Stokes, p. 76; pl. 4: fig. 6; pl. 8: figs 6-7

1977 *Micraster coranguinum rostratus* (Mantell); Stokes, p. 809; pl. 108: figs 4-6

1977 *Micraster coranguinum* (Leske); Stokes, p. 809

1977 *Micraster coranguinum simpsoni* Stokes; Stokes, p. 810; pl. 109: 4-6

1977 *Micraster westlakei* Stokes; Stokes, p. 814; pl. 109: figs 1-3

1993 *Micraster coranguinum* (Leske); Rose & Cross, text-figs 1, 5, 6

1994 *Micraster coranguinum* (Leske); Cross & Rose, text-fig. 1

2002 *Micraster coranguinum* (Leske); Smith & Wright, p. 293; pl. 60: figs 6-8

2007 *Micraster coranguinum* (Leske); Olszlewska-Nejbert, p. 52; pl. 30: fig. 3

***Micraster cortestudinarium* group**

This group is characterized by:

1. Test approximately as broad as long.
2. Paired petals with sutures visible or with broad groove running down the midline.
3. Peristome at approximately 1/5 of test length from anterior margin.
4. Labrum prominent, but not to the same extent as in the *M. coranguinum* group.
5. Periproct at approximately 2/3 of test height from the base.
6. Periplastronal zones with moderately coarse granulation.

1826 *Spatangus cortestudinarium* Goldfuss, p. 146; pl. 48: fig. 5

1826 *Spatangus gibbus* Lamarck; Goldfuss p. 146; pl. 48: figs 4a-c

1840 *Micraster cor-testudinarium* (Goldfuss); Agassiz, p. 2

1847 *Micraster cor-anguinum* var. *lata* Agassiz & Desor, p. 23

1853 *Micraster cor-anguinum* Leske; d'Orbigny, p. 207

1856 *Micraster cortestudinarium* (Goldfuss); Hébert, pl. 29: fig. 18

1874 *Spatangus cortestudinarium* Goldfuss; Quenstedt, p. 646; pl. 87: fig. 30

1877 *Micraster heberti* Lacvivier, p. 538; pl. 8: figs 1-4

1878 *Micraster cortestudinarium* (Goldfuss); Wright, p. 335; pl. 76: fig. 1a-f (part)

1878 *Spatangus decipiens* Bayle, pl. 156: figs 1-2

1878 *Micraster cor-testudinarium* (Goldfuss); Cotteau, p. 478

1878 *Epiaster brevis* Desor; Barrois, p. 409

1880 *Epiaster schlueteri* Coquand, p. 275

1885 *Epiaster Renati* Gauthier, p. 360; pl. 6: figs 3-5

1887 *Micraster heberti* Lacvivier; Cotteau, p. 660

1889 *Micraster cortestudinarium* (Goldfuss); Friç, p. 99; fig. 126

1892 *Micraster Cayeuxi* Parent, p. 13; pl. 2: fig. 2

1895 *Micraster decipiens* (Bayle); Lambert, p. 217

1895 *Micraster gosseleti* Cayeux; Lambert, p. 229

1895 *Micraster heberti* Lacvivier; Lambert, p. 212

1895 *Micraster icaunensis* Lambert, p. 235

1895 *Micraster meridianensis* Cotteau; Lambert, p. 223

1895 *Spatangus gibbus* Lamarck; Lambert, p. 182

1895 *Micraster renati* (Gauthier); Lambert, p. 226

1899 *Micraster cortestudinarium* (sub-group) (Goldfuss); Rowe, p. 534; pl. 35: line 5, figs 1-6

1907 *Micraster decipiens* (Bayle); Valette, p. 179

1907 *Micraster (Gibbaster) icaunensis* Lambert; Valette, p. 136

1907 *Micraster (Isomicraster) renati* (Gauthier); Valette, p. 162

1907 *Micraster (Gibbaster) gauthieri* Parent; Valette, p. 167

1907 *Micraster normanniae* Bucaille; Valette, p. 168

1907 *Micraster (Gibbaster) gosseleti* Cayeux; Valette, p. 169

1920a *Micraster douvillei* Lambert, p. 8; pl. 2: figs 1-2

1920a *Micraster larteti* Munier-Chalmas; Lambert, p. 4

1920a *Micraster proclivus* Lambert, p. 6

1920a *Gibbaster heberti* (Lacvivier); Lambert, p. 15

1920a *Micraster icaunensis* Lambert; Lambert, p. 3

1920a *Micraster gosseleti* Cayeux; Lambert, p. 3

1920a *Micraster coranguinum* Leske; Lambert, p. 7

1922 *Micraster proclivus* Lambert; Lambert, p. 19; pl. 2: figs 5-6

1922 *Micraster douvillei* Lambert; Lambert, p. 20; pl. 2: figs 1-2

1927a *Micraster larteti* Munier-Chalmas; Lambert, p. 46

1934 *Micraster cortestudinarium* (Goldfuss); Andert, p. 76; pl. 18: figs 19-20

1959 *Micraster cortestudinarium* Goldfuss; Mosvkin & Poslavskaya, p. 280; pl. 19: fig. 2; pl. 20: figs 1a-d; text-fig. 93

1959 *'Micraster' heberti* Lacvivier; Mosvkin & Poslavskaya, p. 288-289; pl. 25: figs 3 a-c, 4 a-b; text-fig. 105

1964 *Epiaster brevis* Desor; Arnold, p. 492

1964 *Micraster carinatus* Dzabarov p. 53; pl. 18: fig. 1

1964 *Micraster cortestudinarium* (Goldfuss); Dzabarov, p. 50; pl. 17: fig. 2

1967 *Micraster decipiens* (Bayle); Cayeux, p. 30; pl. 2: figs 7-7b; pl. 3: fig. 7c

1968 *Micraster cortestudinarium* (Goldfuss); Pasternak *et al.*, 219; pl. 49: figs 5-9; text-fig. 48

1970 *Micraster (Micraster) cortestudinarium* (Goldfuss); Ernst, pl. 17: fig. 3

1972 *Micraster cortestudinarium* (Goldfuss); Ernst, pl. 5: fig. 2

1974 *Micraster decipiens* (Bayle); Devriès *et al.*, p. 197

1974 *Micraster icaunensis* Lambert; Devriès *et al.*, p. 198

1974 *Micraster renati* (Gauthier); Devriès *et al.*, p. 198

1974 *Micraster cortestudinarium* (Goldfuss); Savchinskaya, p. 327; pl. 113: figs 1-6

1974 *Micraster cayeusi* Parent; Ernst & Schulz, p. 34; pl. 2: fig. 5; text-fig. 11

1975 *Micraster cortestudinarium* (Goldfuss); Stokes, p. 67; text-fig. 29h

1975 *Micraster heberti* Lacvivier; Stokes, p. 73; pl. 6: fig. 9; pl. 7: figs 1-4; text-fig. 29o

1975 *Micraster decipiens* (Bayle); Stokes, p. 68

1975 *Micraster douvillei* Lambert; Stokes, p. 68; pl. 4: figs 1-5; text-fig. 29i

1975 *Micraster gosseleti* Cayeux; Stokes, p. 72; pl. 6: figs 1-3; text-fig. 29m

1977 *Micraster decipiens* (Bayle); Stokes, p. 810; pl. 108: figs 1-3

1978 *Micraster decipiens* (Bayle); Robaszynski, pl. 1: figs 1-4

1979 *Micraster* gr. C Amedro & Robaszynski in Amedro *et al.*, p. 291; pl. 25: fig. 2a-d, 3a-d

1981 *Micraster decipiens* (Bayle); Fouray, p. 38; pl. 3: figs 8-10

1984 *Micraster decipiens* (Bayle) morphe cordiforme; David & Fouray, p. 469; figs 7, 9

1985 *Micraster decipiens* (Bayle); Fouray & Pomerol, pl. 1: figs 3, 6, 9; pl. 2: figs 2-5

1991 *Micraster decipiens* (Bayle); Tarkowski, p. 130; pl. 27: fig. 1

1998 *Micraster decipiens renati* (Gauthier); Néraudeau *et al.*, p. 326; text-fig. 4c

2002 *Micraster cortestudinarium* (Goldfuss); Smith & Wright, p. 293; pl. 60: figs 4-5

2007 *Micraster cortestudinarium* (Goldfuss); Olszewska-Nejbert, p. 45, pls 24-26; text-figs 50-52

2007 *Micraster (Micraster) cayeusi* Parent; Olszewska-Nejbert, p. 50; pl. 30: fig. 1

***Micraster leskei* group**

This group is characterized by:

1. Test longer than wide.
2. Test thicker than that of the *M. michelini* group.
3. Test without pronounced sub-anal heel.
4. Paired petals without groove between pore-pairs, but with sutures visible.
5. Peristome situated at 1/3 to 1/4 of test length from the anterior.
6. Labral plate projecting only very feebly.
7. Periplastronal areas finely granular.

8. Periproct high on posterior truncation.

1734 *Spatangus cor anguinum (β) norvagicum* Klein, p. 102; pl. 12: figs C-D (part)

1734 *Spatangus cor anguinum (β) norvagicum productum* Klein, p. 33; pl. 23: figs E-F

1754 *Spatangus coranguinum* var. *(β) norvagicum productum* Klein, pl. 12: fig. G

1778 *Spatangus coranguinum* var. *(β) norvagicum* Klein in Leske, pl. 23: figs E-F (part)

1837 *Micraster leskei* des Moulins, p. 392

1840 *Micraster breviporus* Agassiz, p. 2

1847 *Micraster breviporus* Agassiz; Agassiz & Desor, p. 24

1850b *Micraster corbovis* Forbes, p. 342; pl. 24: figs 3-4

1853-60 *Micraster leskei* Des Moulins; d'Orbigny, p. 215; pl. 869: figs 1-8

1858 *Micraster cor-bovis* Forbes; Desor, p. 367

1858 *Micraster leskei* des Moulins; Desor, p. 366

1857-78 *Micraster tropidotus* Agassiz; Cotteau, p. 359; pl. 76: fig. 4

1872 *Micraster normanniae* Bucaille, p. 14; pl. 6

1873 *Micraster breviporus* Agassiz; de Loriol, p. 369; pl. 31: fig. 5a-d

1874 *Micraster borchardi*; Quenstedt, p. 651; pl. 88: fig. 6

1874 *Micraster leskii* Quenstedt, p. 649; pl. 88: figs 2-4

1874 *Micraster leskii quadratus* Quenstedt, p. 650; pl. 88: figs 5

1876 *Micraster breviporus* Agassiz; Cotteau, p. 352; pl. 75: fig. 1-6

1876 *Micraster breviporus* var. *corbovis* Cotteau, p. 354; pl. 76: fig. 1

1878 *Micraster breviporus* Agassiz; Wright, p. 278; pl. 62a: fig. 3a-b

1878 *Micraster cor-bovis* Forbes; Wright, p. 276; pl. 62A: figs 1, 2a-d

1883 *Micraster normanniae* Bucaille, p. 29; pl. 6: figs 1-7

1885 *Micraster beonensis* Gauthier, p. 356; pl. 6: figs 7-9; pl. 8: figs 1-2

1885 *Micraster sanctae maurae* Gauthier, p. 356; pl. 6: figs 1-6

1887 *Micraster sanctae maurae* Gauthier; Gauthier, p. 227; pl. 4: figs 1-6

1887 *Micraster beonensis* Gauthier; Gauthier, p. 229; pl. 4: figs 7-9; pl. 5: figs 1-2

1887 *Micraster breviporus* var. *corbovis* Cotteau; Gauthier, p. 223

1890 *Micraster breviporus* var. from the chalk of Cornus; Cayeux; p. 136; pl. 3: fig. 1

1895 *Micraster breviporus* Agassiz; Lambert, p. 204

1895 *Micraster corbovis* Forbes; Lambert, p. 194

1895 *Micraster leskei* des Moulins 1837; Lambert, p. 178

1895 *Micraster breviporus* Agassiz; Lambert, p. 204

1895 *Micraster beonensis* Gauthier; Lambert, p. 225

1895 *Micraster sanctae-maurae* Gauthier; Lambert, p. 225

1895 *Micraster normanniae* Bucaille; Lambert, p. 221

1889 *Micraster breviporus* Agassiz; Friç, p. 99: fig. 127

1899 *Micraster leskei* group des Moulins; Rowe, p. 525; pl. 36: fig. 20; pl. 38: figs 1-3

1899 *Micraster leskei – M. praecursor* (intermediate forms), Rowe, p. 528; pl. 36: fig. 3; pl. 38: fig. 4

1899 *Micraster corbovis* Forbes; Rowe, p. 518; pl. 35: figs i1-i4; pl. 39: figs 2-3

1899 *Micraster praecursor* (group) Rowe, p. 530; pl. 35: line 4, fig. 3

1901 *Micraster leskei* des Moulins; Lambert in Grossouvre, p. 966

1901 *Micraster corbovis* Forbes; Lambert in Grossouvre, p. 962

1908 *Micraster leskei* des Moulins; Valette, p. 280

1908 *Micraster corbovis* Forbes; Valette, p. 282

1920a *Micraster cantaber* Lambert, p. 13; pl. 3: figs 8-9

1920a *Micraster coribericum* Lambert, p. 8; pl. 3: figs 3, 5

1925 *Micraster leskei* var. *joviniacesis* Lambert & Thiéry, p. 480-1; pl. 12: fig. 10

1935 *Micraster leskei* des Moulins; Smiser, p. 80; pl. 7: fig. 3

1936 *Micraster leskei* des Moulins; Kongiel, p. 6; pl. 2: figs 5a-b

1959 *'Micraster' leskei* des Moulins; Mosvkin & Poslavskaya, p. 287-288; pl. 24: figs 2 a-d; text-fig. 103

1959 *"Micraster" corbovis* Forbes; Mosvkin & Poslavskaya, p. 286-287; pl. 24: figs 1 a-d; text-fig. 102

1959 *Micraster subglobosus* Poslavskaya in Moskvin & Poslavskaya, p. 280; pl. 19: figs 1a-c; text-fig. 92

1964 *Micraster leskei* des Moulins; Dzabarov, p. 47; pl. 16: fig. 3; pl. 17: fig. 1

1964 *Micraster corbovis* Forbes; Dzabarov, p. 45; pl. 16: fig. 2

1966 *Micraster leskei* des Moulins; Raabe, p. 111; pl. 10: fig. 2

1966 *Micraster leskei* des Moulins; Cayeux, p. 38; pl. 2: fig. 12a-d

1967 *Micraster corbovis* Forbes; Cayeux, p. 39; pl. 4: fig. 13

1967 *Micraster normanniae* Bucaille; Cayeux, p. 35; pl. 3: fig. 8a-c

1968 *Micraster corbovis* Forbes; Pasternak *et al.*, p. 217; pl. 48: figs 4-6; text-fig. 46

1968 *Micraster leskei* des Moulins; Pasternak *et al.*, p. 218; pl. 49: figs 1-4; text-fig. 47

1970 *Micraster (Micraster) leskei* des Moulins; Ernst, pl. 17: fig. 2

1970 *Micraster (Micraster) corbovis* Forbes; Ernst, pl. 17: fig. 1

1970 *Micraster (Micraster) corbovis* Forbes; Ernst, pl. 17: fig. 1

1972 *Micraster leskei* des Moulins; Ernst, p. pl. 5: fig. 1

1974 *Micraster leskei* des Moulins; Savchinskaya, p. 326; pl. 111: figs 5-9

1974 *Micraster corbovis* Forbes; Savchinskaya, p. 327; pl. 110: figs 1-5; pl. 111: figs 1-4

1974 *Micraster breviporus* Agassiz; Devriès *et al.*, p. 197

1974 *Micraster beonensis* Gauthier; Devriès *et al.*, p. 197

1974 *Micraster normanniae* Bucaille; Devriès *et al.*, p. 198

1975 *Micraster leskei* des Moulins; Stokes, p. 73; text-fig. 29p

1975 *Micraster borchardi* Quenstedt; Stokes, p. 62; text-fig. 29a

1975 *Micraster corbovis* Forbes; Stokes, p. 66

1975 *Micraster normanniae* Bucaille; Stokes, p. 75; text-fig. 29s

1977 *Micraster leskei* des Moulins; Stokes, p. 812; pl. 108: figs 7-9

1977 *Micraster corbovis* Forbes *planus* zone form Stokes, p. 810; pl. 106: figs 1-3

1977 *Micraster corbovis* Forbes *lata* zone form Stokes, p. 810; pl. 106: figs 4-6

1977 *Micraster normanniae* Bucaille; Stokes, p. 812; pl. 107: figs 1-3, 7-9

1978 *Micraster leskei* des Moulins; Robaszynski, pl. 1: figs 8-14

1979 *Micraster* gr. A and gr. B Amedro & Robaszynski in Amedro *et al.*, p. 192; pl. 24: figs 1-3

1981 *Micraster leskei* des Moulins; Fouray, p. 30; pl. 1: figs 11-16

1981 *Micraster leskei* des Moulins; Fouray, p. 32; pl. 2: figs 1-4; pl. 3: figs 1-4

1981 *Micraster normanniae* Bucaille; Fouray, p. 37; pl. 3: figs 5-7

1984 *Micraster leskei* des Moulins; David & Fournay, p. 467; figs 6, 8, 10

1984 *Micraster decipiens* morphe *normanniae* Bucaille; David & Fouray, p. 468, fig. 16

1985 *Micraster leskei* des Moulins; Fouray & Pomerol, pl. 1: figs 1, 4, 7; pl. 2: figs 1, 8

1985 *Micraster decipiens* (Bayle) morphe *normanniae* Bucaille; Fouray & Pomerol, pl. 1: figs 2, 5, 8

1991 *Micraster leskei* des Moulins; Tarkowski, p. 130; pl. 26: figs 1-3

1991 *Micraster leskei* des Moulins; Fouray & Tarkowski, p. 216; pl. 1: figs 1-6; pl. 2: figs 1-2

2002 *Micraster leskei* des Moulins; Smith & Wright, p. 293; pl. 60: figs 1-3

2007 *Micraster (Micraster) leskei* des Moulins; Olsezewska-Nejbert p. 28; pls 16-21; text-figs 38-45

2007 *Micraster (Micraster) corbovis* Forbes; Olsezewska-Nejbert p. 38; pls 22-23; text-figs 46-47

2007 *Micraster normanniae* Bucaille; Olszewska-Nejbert, p. 42; pl. 23; text-figs 48-49

Micraster michelini group

This group is characterized by:

1. Very thin test (usually around 0.4mm in thickness).
2. Test with a marked sub-anal heel.
3. Peristome situated at approximately 1/3 of test length from the anterior margin.
4. Labrum projecting only very feebly.
5. Periproct situated high on the posterior truncation.
6. Periplastronal areas smoothly granular.
5. A sub-anal fasciole may be present or absent.

1840 *Micraster distinctus* Agassiz, p. 2 (*nomen dubium*)
1847 *Micraster michelini* Agassiz & Desor, p. 23
1853-60 *Epiaster distinctus* (Agassiz & Desor); d'Orbigny, p. 196; pl. 861
1853-60 *Micraster michelini* Agassiz; d'Orbigny, p. 205; pl. 866
1853-60 *Micraster laxoporus* d'Orbigny, p. 217; pl. 870
1858 *Micraster michelini* Agassiz; Desor, p. 363; pl. 41: figs 5-8
1859 *Micraster michelini* Agassiz; Cotteau & Triger, p. 244; pl. 39
1869 *Micraster laxoporus* d'Orbigny; Cotteau & Triger, p. 324; pl. 55: figs 1-4
1869 *Micraster latiporus* Cotteau in Cotteau & Triger, p. 385; pl. 64: figs 1-3
1880 *Micraster incisus* Coquand, p. 272
1881 *Micraster incisus* Coquand; Gauthier in Cotteau *et al.* p. 57
1895 *Micraster incisus* Coquand; Lambert, p. 247
1895 *Micraster latiporus* Cotteau; Lambert, p. 208
1895 *Micraster laxoporus* d'Orbigny; Lambert, p. 195
1895 *Micraster laxoporus* var. *campaniensis* Lambert, p. 196
1895 *Micraster laxoporus* var. *duranica* Lambert, p. 196
1895 *Micraster michelini* Agassiz; Lambert, p. 192
1895 *Micraster caretonensis* Lambert, p. 240
1899 *Micraster corbovis* Forbes; Rowe, p. 518; pl. 39: figs 1-3

1920a *Micraster michelini* Agassiz; Lambert, p. 3

1925 *Micraster micranthus* Lambert & Thiéry, p. 481

1935c *Micraster burgiensis* Lambert, p. 518; pl. 57: 5-8

1968 *Epiaster distinctus* (Agassiz & Desor); Pasternak *et al.*, pl. 48: figs 1-3

1977 *Epiaster michelini* (Agassiz); Stokes, p. 806; pl. 107: figs 4-6, 10-11; text-fig. 1a-b

1977 *Epiaster laxoporus* (d'Orbigny); Stokes, p. 808; pl. 109: figs 7-9; text-fig. 1c-e

1988 *Micraster distinctus* Agassiz & Desor; Smith *at al.*, p. 170; pl. 38: fig. 3; pl. 39: figs 1-4; text-figs 66-67

2007b *Micraster laxoporus* d'Orbigny; Gallemí *et al.*, text-fig. 10a-b

2007b *Micraster burgiensis* Lambert; Gallemí *et al.*, text-fig. 10c-h

2007 *Micraster* cf. *distinctus* Agassiz & Desor; Olszewska-Nejbert, p. 28; pl. 28: fig. 1

***Micraster turonensis* group**

Figure 2.5.1 F, K

This group is distinguished by:

1. Broad, sub-gibbous form.
2. Numerous pore-pairs in paired petals.
3. Peristome situated at approximately 1/5 of test length from the anterior margin.
4. Peristome at approximately 2/3 of test height from the base.
5. Periplastronal areas with coarse granules.

1872 *Micraster intermedius* Bucaille, p. 16; pl. 7

1878 *Spatangus turonensis* Bayle, pl. 156: figs 3-4

1883 *Micraster cortestudinarium* Goldfuss; Cotteau, p. 164

1895 *Micraster intermedius* Bucaille; Lambert, p. 244

1895 *Micraster grossouvrei* Lambert, p. 245

1895 *Micraster arnaudi* Lambert, p. 244

1895 *Micraster turonensis* (Bayle); Lambert, p. 212

1920a *Micraster coniacensis* Lambert, p. 36

1969 *Micraster coranguinum intermedius* Bucaille; Cayeux, p. 6; pl. 1: figs 1-4

1975 *Micraster turonensis* (Bayle); Stokes, p. 80; pl. 11: figs 7-8; pl. 12: figs 1-3

Micraster rogalae group

This group is characterized by:

1. Broad, flat form.
2. Anterior ambulacrum with the outer pore of each pore-pair elongate.
3. Thin test.
4. Peristome situated at approximately 1/5 of test length from the anterior margin.
5. Labrum does not completely cover the mouth.
6. Distinct sub-anal fasciole.

1909 *Micraster rogalae* Nowak, p. 876; pl. 46: figs 1-2

1911 *Micraster belgicus* Lambert, p. 5; pl. 1: figs 1-3

1935 *Gibbaster belgicus* Lambert; Smiser, p. 83

1959 *'Micraster' rogalae* Nowak; Mosvkin & Poslavskaya, p. 288; pl. 24: figs 3; pl. 25: figs 1,2; text-fig. 104

1963 *Micraster rogalae* Nowak; Ernst, p. 105; pl. 14: figs 1a-d, 2

1966 *Micraster roagalae* Nowak; Ernst, p. 125

1968 *Micraster rogalae* Nowak; Pasternak *et al.*, p. 222; pl. 50: figs 5-6

1974 *Micraster rogalae* Nowak; Ernst & Schulz, p. 32; pl. 2: fig. 3; pl. 3: figs 1-4; text-figs 7, 10

1968 *Micraster (Gibbaster) belgicus* Lambert; Maczynska, p. 136; pl. 12: figs 7-9; pl. 13: figs 1-2; pl. 15: fig. 2a-b; pl. 16: figs 1a-2e

1975 *Micraster rogalae* Nowak; Stokes, p. 77

1979 *Micraster rogalae* Nowak; Hynda & Maczynsca, p. 23; pl. 3: fig. 3; pl. 4: fig. 1; pl. 5: figs 1-3; pl. 6: fig. 1; text-figs 3-4

1982 *Micraster rogalae* Nowak; Savchinskaya, p. 239; pl. 29: fig. 2

2007 *Micraster (Micraster) rogalae* Nowak; Olszewska-Nejbert, p. 55; pl. 27: fig. 2; pl. 28-29; text-fig. 54

2007 *Micraster (Micraster) praerogalae* Olszewska-Nejbert, p. 53; pl. 27: fig. 1; text-fig. 54

***Micraster schroederi* group**

Figure 2.5.1 E, J

This group is characterized by:

1. Peristome practically marginal.
2. Labrum elongate, broadest anteriorly, covering the mouth.
3. Paired petals with visible sutures or broad groove along the mid-line.
4. Anterior ambulacrum without well-developed petal.

1822 *Spatangus coranguinum* Leske; Brongniart & Cuvier in Brongniart, p. 388; pl. 4: fig. 11

1840 *Spatangus cuneatus* Hagenow, p. 654; pl. 9: fig. 5

1847 *Micraster matheroni* Desor in Agassiz & Desor, p. 130

1856 *Micraster brongniarti* Hébert, p. pl. 29: fig. 14

1858 *Micraster cor-columbarium* Desor, p. 365

1858 *Micraster brongniarti* Hébert; Desor, p. 365

1859 *Micraster matheroni* Desor; d'Orbigny, p. 203; pls 864-5

1869 *Micraster glyphus* Schlüter, p. 13; pl. 1: fig. 2

1874 *Micraster coranguinum* Leske; Quenstedt, p. 642; pl. 87: figs 28-29

1874 *Micaster glyphus* Schlüter; Cotteau, p. 656; pl. 20: figs 6-10

1874 *Micraster brongniarti* Hébert; Cotteau, p. 655

1876 *Micraster glyphus* Schlüter; Cotteau, p. 269; pl. 84: figs 1-4

1878 *Micraster brongniarti* Hébert; Cotteau, p. 271; pl. 84: figs 5-6

1878 *Micaster glyphus* Schlüter; Cotteau, p. 505; pl. 84: figs 1-4

1887 *Micraster glyphus* Schlüter; Gauthier, p. 233; pl. 6: figs 6-7

1887 *Micraster glyphus* var. Gauthier, p. 234

1887 *Micraster antiquus* Cotteau, p. 642; pl. 16: figs 1-4

1888 *Micraster corcolumbarium* Desor; Seunes, p. 2, 792; pl. 30: fig. 4

1889b *Micraster cor columbarium* Desor; Cotteau, p. 4

1889b *Micraster aturicus* Hébert; Cotteau, p. 7

1890 *Micraster gosseleti* Cayeux, p. 180; pl. 4: fig. 1a-f

1891 *Micraster aturicus* Hébert in Seunes, p. 30; pl. 4; pl. 5: fig. 1.

1891 *Micaster glyphus* Schlüter; Stolley, p. 255; pl. 8: fig. 2a-c

1891 *Micaster gottschei* Stolley, p. 258; pl. 8: fig. 4a-f

1892 *Micraster aturicus* Hébert; Nicklès, p. 110

1892 *Micraster Haasi* Stolley, p. 257; pl. 8: fig. 3

1892 *Micraster schroederi* Stolley, p. 259; pl. 8: fig. 5; pl. 9: fig. 1

1892 *Micraster gauthieri* Parent, p. 10; pl. 2: fig. 1

1895 *Micraster aturicus* Hébert; Lambert, p. 230

1895 *Micraster brongniarti* Hébert; Lambert, p. 199

1895 *Micraster glyphus* Schlüter 1869; Lambert, p. 209

1895 *Micraster marginalis* Arnaud; Lambert, p. 200, 228

1895 *Micraster pseudoglyphus* de Grossouvre; Lambert, p. 199

1895 *Micraster schloenbachi* Desor; Lambert, p. 210

1895 *Micraster corcolumbarium* Desor; Lambert, p. 202

1895 *Micraster matheroni* Desor; Lambert, p. 188

1895 *Micraster arenatus* Sismonda 1843; Lambert, p. 181

1895 *Micraster sismondae* Lambert, p. 200

1895 *Micraster antiquus* Cotteau 1887; Lambert, p. 227

1899 *Micraster coranguinum* var. *latior* Rowe, p. 504

1901 *Micaster glyphus* Schlüter; Lambert in Grossouvre, p. 965

1901 *Micraster schroederi* Stolley; Lambert in Grossouvre, p. 968

1902 *Micaster glyphus* Schlüter; Wollemann, p. 32; pl. 7: fig. 4a-e

1903 *Micraster* cf. *schroederi* Stolley; Savin, p. 26

1903 *Micraster coranguinum* Leske; Savin, p. 25

1903b *Micraster sismondai* Lambert, p. 16

1907 *Micaster schroederi* Stolley; Valette, p. 140

1907 *Micaster brongniarti* Hébert; Valette, p. 141

1911 *Micraster brongniarti* Hébert; Lambert, p. 38

1911 *Micraster schroederi* Stolley; Lambert, p. 52; pl. 1: fig. 6

1911 *Micraster gottschei* Stolley; Lambert, p. 13; pl. 1: fig. 5

1920a *Micraster matheroni* Desor; Lambert, p. 4

1921 *Micraster grimmensis* Nietsch, p. 20; pl. 10: figs 8-9

1927a *Micraster aturicus* Hébert; Lambert, p. 48

1927a *Micraster corcolumbarium* Desor; Lambert, p. 47; pl. 3: figs 17-18

1935 *Micraster coranguinum* var. *schroederi* Stolley; Smiser, p. 82

1937 *Micraster glyphus* var. *sismondai* Lambert; Lambert & Charles, p. 394

1955 *Micraster* cf. *decipiens* (Bayle); Szörenyi, p. 255; pl. 21: figs 11, 13

1959 *Micraster brongniarti* Hébert; Mosvkin & Poslavskaya, p. 284; pl. 22: figs 3 a-e; text-fig. 98

1959 *Micraster schroederi* Stolley; Mosvkin & Poslavskaya, p. 282-283; pl. 21: figs 2 a-e; text-fig. 96

1959 *Micraster rostratus* (Mantell); Mosvkin & Poslavskaya, p. 282; pl. 21: fig. 1; text-fig. 95

1959 *Micraster grimmensis* Nietsch; Moskvin & Poslavskaya, p. 284; pl. 22: fig. 4; text-fig. 99

1959 *Micraster coravium* Poslavskaya in Mosvkin & Poslavskaya, p. 283; pl. 22: figs 1a-e, 2a-b; text-fig. 97

1964 *Micaster glyphus* Schlüter; Giers, p. 227

1968 *Micraster (Micraster) bibicensis* Maczynska, p. 129-130, 168; pl. 13: figs 1a-4; text plate 10: figs 1-4

1968 *Micraster (Micraster) schroederi schroederi* Stolley; Maczynska, p. 112; text-pl. 3: fig. 5; text-pl. 4: figs 1-8; pl. 4: fig. 1a-f; pl. 5: fig. 1a-d

1968 *Micraster (Micraster) schroederi planus* Maczynska, p. 116-118, 168; pl. 5: figs 2a-c; pl. 6: figs1a-2d; pl. 7: figs 1a-e; text plate 5: figs 1-3; text plate 6: figs 1-3

1968 *Micraster (Micraster) coranguinum* Leske; Maczynska, p. 108; text-pl. 2: figs 1-3; text-pl. 3: figs 1-4; pl. 3: figs 1-3.

1968 *Micraster (Micraster) glyphus* Schlüter; Maczynska, p. 118; text-pl. 6: figs 4-7; text-pl. 7: figs 1-8; pl. 8: figs 1a-3c; pl. 9: figs 1a-5; pl. 10: fig. 1a-d

1968 *Micraster (Micraster) brongniarti* Hébert; Maczynska, p. 124; text-pl 8; text-pl. 9: figs 1-6; pl. 11: figs 1a-5e; pl. 12: figs 2a-4

1968 *Micraster (Paramicraster)* sp. Maczynska, p. 160; text-pl. 12: figs 3-6; pl. 28: fig. 2a-c

1968 *Micraster (Paramicraster) latior* Rowe; Maczynska, p. 158; pl. 22: figs 1-2; pl. 26: fig. 1a-e; pl. 27: fig. 1a-f; pl. 28: fig. 1a-b

1968 *Micraster (Paramicraster) cracoviensis* Maczynska, p. 155-157, 168; pl. 24: figs 1a-e; pl. 25: 1a-d; text plate 21: figs 1-4]

1968 *Micraster* cf. *schroederi* Stolley; Pasternak *et al.*, p. 223; pl. 50: fig. 7

1970 *Micraster glyphus* Schlüter; Ernst, pl. 17: fig. 4

1974 *Micraster bucailli* Parent; Ernst & Schulz, p. 28; pl. 1: figs 1-2; pl. 2: figs 1, 4; text-figs 7, 8a, 9a-c

1975 *Micraster schroederi* Stolley; Stokes, p. 78; pl. 9: figs 5-7; pl. 10: figs 1-2; text-fig. 30c

1975 *Micraster sismondai* Lambert; Stokes, p. 79; pl. 10: figs 7-9; pl. 11: figs 1-2; text-fig. 30d

1975 *Micraster glyphus* Schlüter; Stokes, p. 70; text-fig. 29l

1975 *Micraster grimmensis* Nietsch; Stokes, p. 72; pl. 6: figs 4-8; text-fig. 29n

1975 *Micraster aturicus* Hébert; Stokes, p. 61; pl. 1: figs 1-3

1975 *Micraster brongniarti* Hébert; Stokes, p. 63; pl. 1: figs 4-8; text-fig. 29c

1975 *Micraster coravium* Poslavskaya; Stokes, p. 66; pl. 3: figs 9-10; text-fig. 29g

1975 *Micraster corcolumbarium* Desor; Stokes, p. 67, pl. 3: figs 6-8

1975 *Micraster antiquus* Cotteau; Stokes, p. 61

1979 *Micraster aturicus* Hébert; Gongadze, tables 1-2

1987 *Micraster schroederi* Stolley; van der Ham *et al.*, p. 33; pl. 22

1995 *Micraster* gr. *stolleyi* (Lambert); Gallemí *et al.* table 1

1999 *Micraster aturicus* Hébert; Jagt, p. 10; pl. 1: figs 16-18; pl. 2: figs 9-14.

1999 *Micraster* gr. *schroederi/glyphus* Jagt, p. 10, pl. 2: figs 1-3, 7, 8.

2000 *Micraster (Micraster) grimmensis* Nietsch; Smith & Jeffery, p. 298; text-fig. 126

2000 *Micraster (Micraster) schroederi* Stolley; Smith & Jeffery, p. 297; text-fig. 125

2000 *Micraster* (*Micraster*) *aturicus* Hébert; Smith & Jeffery, p. 298

2001 *Micraster corcolumbarium* Desor; Néraudeau & Odin, p. 628, pl. 4: figs 85, 86.

2001 *Micraster aturicus* Hébert in Seunes; Néraudeau & Odin, p. 628; pl. 4: figs 79-81.

2004 *Micraster aturicus* Hébert in Seunes; Kroh & Jagt, p. 566; pl. 8: figs 1-3, 6

2004 *Micraster corcolumbarium* Desor; p. Kroh & Jagt, p. 566; pl. 8, Figs 4, 5

2007 *Micraster (Micraster) bucailli* Parent; Olszewska-Nejbert, p. 51; pl. 30: fig. 2

2007a *Micraster matheroni* Desor; Gallemí text-fig. 9j-l

Genus ***CYCLASTER*** Cotteau, 1856

[=*Brissopneustes* Cotteau, 1887, type species *Brissopneustes vilanovae* Cotteau, 1887; =*Isopneustes* Seunes, 1888 *non* Pomel, 1883]

TYPE SPECIES

Cyclaster declivus Cotteau, 1856 by original designation. (Eocene, France.)

DIAGNOSIS

Apical system with three gonopores (no pore in genital plate 2); strong sexual dimorphism of gonopore size. Anterior ambulacrum with enlarged pore-pairs and in a very weak groove. Peristome over 15% of test length from the anterior margin and only partially covered by weakly projecting labrum. Subanal fasciole always present; peripetalous fasciole sometimes present.

REMARKS

Brissopneustes and *Cyclaster* have been distinguished on the presence or absence of a peripetalous fasciole. However, Smith & Jeffery (2000) pointed out that this character is variably developed within individual species and so synonymized the two genera. The taxonomy of *Cyclaster* has been the subject of a careful revision by Jeffery (1998) and Smith & Jeffery (2000); their scheme is largely followed here.

Cyclaster galei Jeffery, 1997

1997 *Cyclaster galei* Jeffery, p. 704, pl. 10: figs 5-8; text-figs 16, 18a-c
2000 *Cyclaster galei* Jeffery; Smith & Jeffery, p. 316

DIAGNOSIS

Test narrow (test width approximately 75% of test length) with rectangular outline and flat oral and apical surfaces. Paired petals short and almost flush, the anterior pair diverges at approximately 90°.

REMARKS

The characteristic rectangular outline of this species distinguishes it from all Cretaceous congeners apart from *C. ruegensis*, from which it differs in having a much narrower test and less divergent anterior paired petals.

OCCURRENCE

Maastrichtian of Mangyshlak, Kazakstan.

Cyclaster gindrei (Seunes, 1888)

1888 *Isopneustes gindrei* Seunes, p. 795, pl. 28: fig. 2

1940 *Cyclaster pyriformis* Rouchadzé, p. 127, 154, 174; pl. 3: fig. 6

2000 *Cyclaster gindrei* (Seunes); Smith & Jeffery, p. 312

DIAGNOSIS

Inflated, globular test with rectangular outline, strong posterior keel. Anterior ambulacrum in shallow groove that cuts the ambitus. Apical system anterior. Paired petals short, with anterior pair longer than posterior pair. Labral plate long and narrow.

OCCURRENCE

Maastrichtian-Danian of Georgia (Rouchadzé 1940); Maastrichtian of Tremp, Spain (Smith & Jeffery 2000). Also known from the Danian of the French Pyrenees the northern Caucasus and the Transcaspian region (Smith & Jeffery 2000 and references therein).

Cyclaster heberti (Nicklès, 1892)

1892 *Isopneustes heberti* Nicklès, p. 111; pl. 9: figs 12-13

1973 *Isopneustes heberti* Nicklès; Radig, p. 62; pl. 10: fig. 8; pl. 11: figs 1-2

1995 *Isopneustes heberti* Nicklès; Gallemí *et al.*, table 1

1995 *Isopneustes heberti*? Nicklès; Gallemí *et al.*, table 1

1995 *Isopneustes* sp. Gallemí *et al.*, table 1

?1996 *Isopneustes* sp. Wilmsen *et al.*, fig. 7

2000 *Cyclaster heberti* (Nicklès); Smith & Jeffery, p. 314; text-fig. 130g

DIAGNOSIS

Low, coffin-shaped test with a frontal groove that cuts the ambitus only weakly. Paired ambulacra slightly sunken with numerous elongate pore-pairs. Labral plate long and narrow. Peristome surrounded by prominent rim. Complete peripetalous fasciole present.

OCCURRENCE

Maastrichtian of Alicante, Spain (Nicklès 1892; Gallemí *et al.* 1995; Smith & Jeffery 2000) and Santander, Spain; Campanian of Navarro, Spain (Radig 1973).

Cyclaster integer (Seunes, 1888)

1888 *Isopneustes integer* Seunes, p. 798; pl. 28: fig. 1

1888 *Isopneustes munieri* Seunes, p. 798; pl. 28: fig. 4

1940 *Cyclaster pygmeus* Rouchadzé, p. 129, 155, 174; pl. 3: fig. 7

1959 *Cyclaster integer* (Seunes); Mosvkin & Poslavskaya, p. 291; pl. 26: figs 4-5; text-fig. 107

1960 *Cyclaster integer* (Seunes); Poslavskaya & Mosvkin, p. 69; pl. 5: figs 4-5; text-fig. 20

2000 *Cyclaster integer* (Seunes); Smith & Jeffery, p. 314-315; text-fig. 130d,f

DIAGNOSIS

Inflated coffin-shaped test with broad shallow anterior groove and slightly carinate upper surface. Paired petals short and sub-equal in length with small round pore-pairs. Labral plate long and narrow. Complete peripetalous fasciole present.

OCCURRENCE

Maastrichtian to Danian of the French Pyrenees (Seunes 1888); Maastrichtian of Azerbaijan (Rouchadzé 1940); Late Maastrichtian and Early Danian of the northern Caucasus and Transcaspian region (Mosvkin & Poslavskaya 1959; Poslavskaya & Movskin 1960). Also from the Danian of Georgia, Kazakhstan, Madagascar and Denmark (Smith & Jeffery 2000 and references therein).

Cyclaster pfenderae Lambert, 1936

1936 *Cyclaster pfenderae* Lambert, p. 27; pl. 4: figs 17-19
2000 *Cyclaster pfenderae* Lambert; Smith & Jeffery, p. 315; text-fig. 131.

DIAGNOSIS
Low, ovate test with depressed sutures between plates. Well-developed paired petals with anterior pair slightly longer than posterior. Peristome surrounded by distinct rim. Labral plate broad. Dense pustular tubercles on upper surface. Complete peripetalous fasciole.

OCCURRENCE
Maastrichtian of north-west Madagascar (Lambert 1936).

Cyclaster platornatus Kutscher, 1978

1978 *Cyclaster platornatus* Kutscher, p. 1028; pl. 3: figs 1-5
1982 *Cyclaster platornatus* Kutscher; Nestler, p. 82
1987 *Cyclaster platornatus* Kutscher; Jagt & Michels, p. 58; figs 1-6
1987 *Cyclaster platornatus* Kutscher; van der Ham *et al.*, p. 34
1990 *Cyclaster platornatus* Kutscher; Jagt & Michels, p. 181; figs 1-6
2000 *Cyclaster platornatus* Kutscher; Jagt, p. 286, pl. 24: figs 10-12
2000 *Cyclaster platornatus* Kutscher; Smith & Jeffery, p. 315

DIAGNOSIS

Test oval in outline when viewed from above. Paired petals well-developed and sunken with anterior pair longer than posterior. Large kidney-shaped peristome surrounded by a prominent rim. A few scattered pustular tubercles on upper surface. Complete peripetalous fasciole.

OCCURRENCE

Early Maastrichtian of Rügen, Germany (Kutscher 1978; Nestler 1982); early Late Maastrichtian of Haccourt, Belgium (Jagt & Michels 1987, 1990).

Cyclaster ruegensis (Kutscher, 1978)

1978 *Brissopneustes rügensis* Kutscher, p. 1027, pl. 2
2000 *Cyclaster ruegensis* (Kutscher); Smith & Jeffery, p. 316

DIAGNOSIS

Large species with a broad rectangular outline when viewed from above. Short, equal paired petals that are almost flush. Peripetalous fasciole absent.

OCCURRENCE

Early Maastrichtian of Rügen, Germany (Kutscher 1978).

Genus ***DIPLODETUS*** Schlüter, 1900

TYPE SPECIES

Diplodetus brevistella Schlüter, 1900, by subsequent designation of Lambert & Thiéry (1925).

DIAGNOSIS

Test longer than wide with high point posterior of the apical system. Anterior ambulacrum sunken near apical system but becomes almost flush by the ambitus. Apical system ethmophract with four gonopores. Paired petals sunken with elongate pores. Peristome at 25-33% of test length from the anterior margin and only slightly covered by the labral projection. Subanal fasciole present.

REMARKS

Distinguished from other micrasterid genera by having four gonopores, short sunken paired petals and a test that is longer than broad and highest posteriorly.

Diplodetus brevistella (Schlüter, 1900)

1900 *Diplodetus brevistella* Schlüter, p. 364; pl. 15: figs 3-5
1925 *Diplodetus schlueteri* Lambert & Thiéry, p. 484

DIAGNOSIS

Test of variable form with a very broad diffuse peripetalous fasciole.

REMARKS

There are a number of specimens from the Santonian and Campanian of Western Europe that might be conspecific but are of variable form and are generally poorly preserved and require further study (see Jagt 2000). These specimens, which I have been unable to examine as part of this thesis, include *D. cretaceus* (Schlüter, 1869 – see Schlüter 1900, p. 366; pl. 15: fig. 2), *D. carinatus* (Anthula, 1899, p. 65; pl. 2: fig. 9), *D. gaudryi* (Cottreau, 1908b p. 30; pl. 5: fig. 7), *D. pyrenaicus* Lambert, 1900 (p. 703; pl. 24: fig. 51), *D. recklinghausenensis* (Schlüter, 1900, p. 368; pl. 15: fig. 1), *D. minor* (Schlüter, 1900, p. 369; pl. 16: figs 3-5), *D. cavifer* (Schlüter, 1900, p. 371; pl. 17: figs 3-4) and *D. cordiformis* (Schlüter, 1900, p. 372; pl. 16: figs 1-2).

OCCURRENCE

Campanian of the Maastricht region (Schlüter 1900) and possibly from the Santonian to Campanian of other parts of Western Europe.

Diplodetus americanus (Stephenson, 1941)

Figure 2.5.1 C-D, L

1941 *Micraster (Plesiaster) americanus* Stephenson, p. 69; pl. 7: figs 1-4

1953 *Micraster americanus* Stephenson; Cooke, p. 38; pl. 15: figs 10-13

2000 *Diplodetus americanus* (Stephenson); Smith & Jeffery, p. 306; text-figs 129d-e

DIAGNOSIS

Test with weak anterior groove and vertical truncate posterior face. Petals sharply defined and deeply sunken. Anterior paired petals diverge at approximately 100° and are approximately 1.25 times the length of the posterior pair. Labral plate more than twice as long as wide. Peristome at about 25% of test length from the anterior margin. Subanal and partial peripetalous fascioles present.

REMARKS

As crystallographic analysis reveals that this species is non-planktotrophic, it seems likely that the deep and sharply defined petals may have acted as marsupia.

OCCURRENCE

Late Campanian to Late Maastrichtian of Texas, Arkansas and Mississippi, USA.

Diplodetus bucardium (Goldfuss, 1829)

1829 *Spatangus bucardium* Goldfuss, p. 157; pl. 49: fig. 1
1899 *Plesiaster bucardium* (Goldfuss); Schlüter, p.119; pl. 9: figs 1-4
1987 *Diplodetus bucardium* (Goldfuss); van der Ham *et al.*, p. 34; pl. 23: fig. 2
1998 *Diplodetus bucardium* (Goldfuss); Indeherberge *et al.*, p. 687, text-fig. 3
2000 *Diplodetus bucardium* (Goldfuss); Jagt, p. 289, pl. 26: figs 6-7
2000 *Diplodetus bucardium* (Goldfuss); Smith & Jeffery, p. 306-308

DIAGNOSIS
Test only slightly longer than wide with vertically truncate posterior and a distinct frontal notch. Labrum approximately 1.5 times as long as wide. Deeply sunken paired petals with the anterior pair diverging at approximately 105° and being approximately 1.4 times as long as the posterior pair. Labral plate approximately 1.5 times longer than wide. Peristome at approximately 25% of test length from the anterior margin. Subanal and partial peripetalous fasciole present.

OCCURRENCE
Early Maastrichtian of the Maastricht region (van der Ham *et al.* 1987; Indeherberge *et al.* 1998; Jagt 2000).

Diplodetus coloniae (Cotteau, 1877)

1877 *Cyclaster coloniae* Cotteau, p. 70; pl. 7: figs 33-34
1892 *Cyclaster coloniae* Cotteau; Nicklès, p. 110
2000 *Diplodetus coloniae* (Cotteau); Smith & Jeffery, p. 309-310; text-fig. 129a-b

DIAGNOSIS

Test ovate with virtually no anterior depression and a vertically truncate posterior face. Anterior paired petals shallow, very divergent (approximately 140-150°) and approximately the same length as the posterior pair. Peristome at approximately 25% of test length from the anterior margin. Subanal fasciole present.

OCCURRENCE

Maastrichtian of Alicante, Spain (Nicklès 1892). Also known from the Palaeocene of Belgium, the French Pyrenees and the Crimea (Smith & Jeffery 2000 and references therein).

Diplodetus duponti (Lambert, 1911)

1902 *Micraster (Brissopneustes) maestrichtensis* Lambert, p. 122; pl. 6: figs 1-4; text-fig. 1 (*nomen dubium*)
1911 *Micraster duponti* Lambert, p. 50; pl. 2: fig. 21; pl. 3: figs 1-2
1911 *Micraster maestrichtensis* Lambert; Lambert, p. 52
1935 *Micraster duponti* Lambert; Smiser, p. 81
1987 *Diplodetus duponti* (Lambert); van der Ham *et al.*, p. 34; pl. 24: fig. 1
1992 *Diplodetus duponti* (Lambert); van der Ham & van Birgelen, p. 150; pl. 4: figs 7-8
1998 *Diplodetus duponti* (Lambert); Indeherberge *et al.*, p. 688, text-fig. 5
2000 *Diplodetus duponti* (Lambert); Jagt, p. 289, pl. 27: figs 1-2
2000 *Diplodetus duponti* (Lambert); Smith & Jeffery, p. 308; text-fig. 129f

DIAGNOSIS

Test with a shallow, yet well defined, frontal groove and an overhanging truncate posterior. Paired ambulacra moderately sunken, the anterior pair diverge at approximately 120° and are around 1.5 times the length of the posterior pair. Labral plate approximately 1.5 times as long as wide. Peristome about 25% of test length from the anterior margin and is strongly

labiate with a prominet rim. Subanal fasciole and possibly very faint peripetalous fasciole present.

REMARKS

Micraster (*Brissopneustes*) *maestrichtensis* has been described from a single specimen, which apparently had three gonopores (Lambert 1902). However, all similar spatangoids from the Maastricht region have three gonopores (Smith & Jeffery 2000) and it seems likely that the specimen is in fact conspecific with *D. duponti*. If this is the case, then the name *M.* (*B.*) *maestrichtensis* would have priority, but as the whereabouts of the specimen is now not known (Jagt 2000) it is considered to be a *nomen dubium* here.

OCCURRENCE

Late Early Maastrichtian and Late Maastrichtian of the Maastricht region, Netherlands and Belgium.

Diplodetus gauthieri Cottreau, 1908b

1908b *Diplodetus gauthieri* Cottreau, p. 174, pl. 3: fig. 7
2000 *Diplodetus gauthieri* Cottreau; Smith & Jeffery, p. 309

DIAGNOSIS

Ovate test with a sloping posterior truncation. Apical system at mid length. Paired petals deeply sunken, anterior pair diverge at approximately 120° and are approximately 1.1 times as long as the posterior pair. Peristome situated at 33% of test length from the anterior margin. Subanal and diffuse peripetalous fascioles present.

OCCURRENCE

Maastrichtian of southwest Madagascar (Besairie 1971). Also from the Danian of northwest Madagascar (Tanaka *et al.* 1979).

Diplodetus nutrix (Lambert in Boule, 1899)

1899 *Epiaster nutrix* Lambert in Boule, p. 132

1903a *Epiaster nutrix* Lambert; Lambert, p. 86; pl. 3: figs 3-5

1906 *Epiaster nutrix* Lambert; Lambert in Boule & Thévénin, p. 52; pl. 2: fig. 5

1908b *Micraster nutrix* (Lambert); Cottreau, p. 169; pl. 4: fig. 4

1922 *Micraster nutrix* (Lambert); Cottreau, p. 117

?1930 *Hemiaster* sp. Besairie, p. 230; pl. 24: fig. 6

2000 *Diplodetus nutrix* (Lambert); Smith & Jeffery, p. 308; text-fig. 129c

2005 *Diplodetus nutrix* (Lambert); Parma & Casadío, p. 1078; text-figs 9.1-9.6, 10.1-10.2

DIAGNOSIS

Test with shallow frontal notch and a sloping posterior truncation. Paired ambulacra deeply sunken, anteriors diverge at approximately 125° and are around 1.5 times longer than the posterior pair. Peristome situated at approximately 33% of test length from the anterior margin.

REMARKS

Smith & Jeffery (2000) identified sexual dimorphism in gonopore size in this species.

OCCURRENCE

Maastrichtian of east (Lambert in Boule & Thévénin 1906) and possibly northwest (Besairie 1930) Madagascar; Maastrichtian to Danian of Argentina (Parma & Casadío 2005).

Diplodetus parvistella (Schlüter, 1899)

1899 *Plesiaster*(?) *parvistella* Schlüter, p. 121; pl. 9: fig. 5

1987 *Diplodetus parvistella* (Schlüter); van der Ham *et al.*, p. 34; pl. 24: fig. 2

1998 *Diplodetus parvistella* (Schlüter); Indeherberge *et al.*, p. 687, text-fig. 4

2000 *Diplodetus parvistella* (Schlüter); Jagt, p. 290; pl. 26: figs 4-5; pl. 27: figs 3-4

2000 *Diplodetus parvistella* (Schlüter); Smith & Jeffery, p. 309

DIAGNOSIS

Low, ovate test with sloping posterior truncation. Apical system at mid length. Paired petals shallow, anterior pair diverge at approximately 105° and are around 1.4 times the length of the posterior pair. Peristome with distict rim situated at approximately 25% of test length from the anterior margin. Subanal and diffuse peripetalous fascioles present.

OCCURRENCE

Late Maastrichtian of the Maastriht region, Netherlands and Belgium (van der Ham *et al.* 1987; Indeherberge *et al.* 1998; Jagt 2000).

***Diplodetus* sp.**

Diplodetus aff. *americanus* (Stephenson); Jagt 2000, p. 188; pl. 26: figs 1-3

REMARKS

These specimens appear to be close to *D. americanus*, but are not sufficiently well preserved to be assigned to this species with confidence.

OCCURRENCE

Uppermost Maastrichtian of the Maastricht region (Jagt 2000).

Genus ***GIBBASTER*** Gauthier, 1887

[=*Isomicraster* Lambert in Grossouvre, 1901; type species *Isomicraster stolleyi* Lambert in Grossouvre, 1901]

TYPE SPECIES

Micraster fastigatus Gauthier, 1887 (=*Micraster gibbus* Desor, 1858), by original designation.

DIAGNOSIS

Test conical in shape. All five ambulacra petaloid. Position of the peristome variable. Periproct below mid-height. Sub-anal fasciole may be present or absent.

REMARKS

Isomicraster has been traditionally considered to differ from *Gibbaster* in lacking a subanal fasciole. However, Ernst (1970) has shown that both are likely to belong to a single lineage. Many of the remarks made for the genus *Micraster* apply equally to *Gibbaster*, which many authors have considered to be a subgenus of *Micraster*. As for *Micraster*, I attempt here to provide a comprehensive list of records that need to be studied by future workers wishing to revise this genus.

***Gibbaster* sp. or spp.**

1791 Un-named Brugières, pl. 156: figs 4-6

1816 *Spatangus gibbus* Lamarck, p. 33

1840 *Micraster cordatus* Agassiz, p. 2

1843 *Micraster arenatus* Sismonda, p. 28; pl. 1: fig. 12

1847 *Micraster cordatus* Agassiz & Desor, p. 23

1847 *Micraster cor-anguinum* var. *major* Agassiz & Desor, p. 23

1847 *Micraster brevis* Desor in Agassiz & Desor, p. 24

1850b *Micraster gibbus* (Lamarck); Forbes, p. 342; pl. 24: figs 5-6

1856 *Micraster desori* Hébert, pl. 29: fig. 17

1856 *Micraster brevis* Desor; Leymerie & Cotteau, p. 346

1858 *Micraster gibbus* (Lamarck); Desor, p. 365

1858 *Micraster brevis* Desor; Desor, p. 364

1858 *Micraster cor-anguinum* var. *géante* Desor, p. 364

1863 *Micraster cortestudinarium* Goldfuss; Cotteau, p. 55

1869 *Epiaster gibbus* (Lamarck); Schlüter, p. 237; pl. 2: fig. 1

1869 *Epiaster brevis* (Desor); Schlüter, p. 240; pl. 2: fig. 2

1870 *Micraster idae* Cotteau, p. 3; pl. 12: figs 4-7

1874 *Micraster gibbus* (Lamarck); Quenstedt, p. 648; pl. 88: fig. 1

1874 *Micraster brevis* Desor; Quenstedt, p. 655, pl. 88: fig. 18

1874 *Micraster* sp. Cotteau, p. 655

1877 *Micraster hebert* de Lacvivier, p. 537; pl. 8

1878 *Spatagus brevis* (Desor); Bayle, pl. 156: figs 5-6

1878 *Epiaster gibbus* (Lamarck); Wright, p. 267

1878 *Epiaster gibbus* (Lamarck); Cotteau, p. 492; pl. 82: fig. 4

1880 *Epiaster anglicus* Coquand, p. 282

1881 *Micraster brevis* Desor; Wright, p. 339; pl. 75: fig. 3a-g

1887 *Micraster brevis* Desor; Cotteau, p. 600

1887 *Micraster (Gibbaster) gibbus* (Lamarck); Gauthier, p. 235

1887 *Micraster fastigatus* Gauthier, p. 237; pl. 6: figs 1-5

1889b *Micraster brevis* Desor; Cotteau, p. 3

1889b *Micraster gourdoni* Cotteau, p. 5; pl. 1: figs 1-2

1892 *Micraster gibbus* (Lamarck); Stolley, p. 260; pl. 9: fig. 2

1895 *Micraster corbaricus* Lambert 1895; Lambert, p. 237

1895 *Micraster fastigatus* Gauthier; Lambert, p. 227

1895 *Micraster gibbus* Lambert, p. 168

1895 *Micraster senonensis* Lambert, p. 239

1895 *Micraster anceps* Lambert, p. 245

1895 *Micraster gourdoni* Cotteau 1889; Lambert, p. 229

1895 *Micraster brevis* Desor; Lambert, p. 182

1895 *Micraster cortestudinarium* (Goldfuss 1826); Lambert, p. 175

1895 *Micraster idae* Cotteau; Lambert, p. 211

1896 *Micraster meunieri*; Lambert, p. 326; pl. 12: figs 1-2

1896 *Micraster fortini* Lambert, p. 328; pl. 12: figs 6-7

1897 *Micraster ciplyensis* Schlüter, p. 19; pl. 2: figs 1-2

1899 *Epiaster gibbus* Lambert; Rowe, p. 534

1901 *Isomicraster stolleyi* Lambert in Grossouvre, p. 959

1902 *Epiaster gibbus* (Lamarck); Wolleman, p. 33

1902 *Micraster corbaricus* Lambert; Lambert, p. 22

1903a *Micraster meunieri* Lambert; Lambert, p. 76-78

1903b *Isomicraster ciplyensis* (Schlüter); Lambert, p. 43; pl. 2: fig. 16

1907 *Micraster anceps* Lambert; Valette, p. 182

1910a *Micraster corbaricus* Lambert; Lambert, p. 814

1910a *Isomicraster dallonii* Lambert, p. 814; pl. 15: figs 13-14

1920a *Micraster corbaricus* Lambert; Lambert, p. 3

1920a *Gibbaster mengaudi* Lambert, p. 14; pl. 2: figs 13-15

1927a *Micraster corbaricus* Lambert; Lambert, p. 46

1927a *Micraster gourdoni* Cotteau; Lambert, p. 48

1927a *Micraster dallonii* Lambert; Lambert, p. 48

1931 *Isomicraster brueti* Lambert, p. 101; pl. 4: figs 8-9

1932 *Isomicraster brueti* Lambert; Lambert, p. 101-102

1932 *Micraster corbaricus* Lambert, p. 73

1935 *Isomicraster stolleyi* (Schlüter); Smiser, p. 82

1935 *Isomicraster ciplyensis* (Schlüter); Smiser, p. 83

1935b *Isomicraster mexicanus* Lambert, p. 371-372; fig. 2

1940 *Isomicraster faasi* Rouchadzé, p. 24-125, 153-154, 173-174; figs 16-17; pl. 3: figs 4a-c

1953 *Isomicraster danei* Cooke, p. 29; pl. 11: figs 11-13

1953 *Isomicraster rossi* Cooke, p. 29; pl. 11: figs 15-16

1953 *Micraster uddeni* Cooke, p. 37-38; pl. 15: figs 6-9

1954 *Micraster (Isomicraster) senonensis* Lambert; Kermack, pl. 24: fig. 13; pl. 25: fig. 15; pl. 26: fig.17

1955 *Micraster (Gibbaster) fastigatus* Gauthier; Szörenyi, p. 256; pl. 21: figs 15-19

1959 *Isomicraster faasi* Rouchadzé; Mosvkin & Poslavskaya, p. 285; pl. 23: figs 1 a-d; text-fig. 100

1959 *"Isomicraster" ciplyensis* (Schlüter); Mosvkin & Poslavskaya, p. 289; pl. 25: fig. 5

1959 *Isomicraster gibbus* (Lambert); Mosvkin & Poslavskaya, p. 286; pl. 23: figs 2 a-d; text-fig. 101

1968 *Micraster (Gibbaster) gibbus* (Lamarck); Maczynska, p. 132; pl. 12: figs 1-6; pl. 14: figs 1a-2d; pl. 15 fig. 1a-e; text-fig. 11: figs 1-3

1968 *Micraster (Gibbaster) fastigatus* Gauthier; Maczynska, p. 138; pl. 13: figs 3-4; pl. 14: figs 1-8; pl. 15: figs 1-5; pl. 17: figs 1a-2c; pl. 18: figs 1a-3b; pl. 19: figs 1a-2

1970 *Micraster (Gibbaster) gibbus* Lamarck; Ernst, pl. 18: fig. 5

1970 *Micraster (Isomicraster) stolleyi* Lambert; Ernst, pl. 18: figs 6-7

1970 *Micraster (Gibbaster)* sp. Ernst, pl. 18: figs 3-4

1972 *Micraster (Gibbaster)* aff. *brevis* Desor; Ernst, pl. 2: fig. 6

1975 *Micraster stolleyi* Lambert; Stokes, p. 79, text-fig. 30f

1975 *Micraster gourdoni* Cotteau; Stokes, p. 72

1975 *Micraster brevis* Desor; Stokes, p. 62; text-fig. 29b

1975 *Micraster mengaudi* (Lambert); Stokes, p. 74; pl. 7: figs 5-7; text-fig. 29q

1975 *Micraster gibbus* (Lamarck); Stokes, p. 70; pl. 5: figs 3-7; text-fig. 29k

1975 *Micraster fastigatus* Gauthier; Stokes, p. 69; pl. 4: figs 7-9; pl. 5: figs 1-2; text-fig. 29j

1977 *Micraster gibbus* (Lamarck); Stokes, p. 812

1981 *Micraster gibbus* (Lamarck); Fouray, p. 41; pl. 4: figs 1-2

2000 *Micraster stolleyi* (Lambert); Jagt, p. 285, pl. 25: figs 7-11

2004 *Micraster stolleyi* (Lambert); Kroh & Jagt, p. 365-366; pl. 8: figs 7, 8

2004 *Pseudogibbaster* sp. Kroh & Jagt, p. 563; pl. 7: figs 1-9; text-figs 8-9
2007a *Micraster brevis* Desor; Gallemí text-fig. 10f-i
2007 *Micraster* (*Gibbaster*) *brevis* Desor; Olszekska-Nejbert, p. 59; pl. 30: fig. 4; pl. 31: figs 1-3; text-fig. 58

Genus ***ISASTER*** Desor, 1858

TYPE SPECIES
Isaster acquitanicus Desor, 1858 (=*Spatangus acquitanicus* Grateloup, 1836), by original designation.

DIAGNOSIS
Test ovate in outline with the anterior margin not cut by a frontal notch. Apical system with 3 gonopores (no pore in genital plate 2). Pore-pairs in the anterior ambulacrum similar to those in the paired petals. Paired petals weakly depressed. Periproct situated low on the posterior face. No fascioles present.

REMARKS
Isaster can be distinguished from all Cretaceous micrasterids other than *Cyclaster* on the basis of having three (rather than four) genital pores. It differs from *Cyclaster* in having no fascioles, pore-pairs in the anterior ambulacrum that are similar to those in the paired ambulacra and a frontal groove that does not cut the ambitus

Isaster aquitanicus (Grateloup, 1836)

1836 *Spatangus aquitanicus* de Grateloup, p. 176, pl. 2: fig. 17
1996 *Isaster* sp. Wilmsen *et al.*, fig. 7
2000 *Isaster aquitanicus* (Grateloup); Smith & Jeffery, p. 317; text-fig. 132

DIAGNOSIS

As for genus.

REMARKS

This species has been distinguished from the Palaeocene species *I. toulai* (Böhm) – the type species of *Ismidaster* - on the basis of having sunken (rather than flush) petals that are less parallel sided. Smith & Jeffery (2000) did not consider these differences sufficient to maintain separate species and placed *I. toulai* under the synonymy of *I. aquitanicus*.

OCCURRENCE

Maastrichtian of the Cabo de Lata Formation of Santander, Cantabria, Spain (Wilmsen *et al.* 1996); Maastrichtian of Alicante, Spain (Smith & Jeffery 2000). Also known from the Palaeocene of Navarra, Spain (Smith *et al.* 1999), and the Crimea, Kazakstan and Turkey (Smith & Jeffery 2000 and references therein).

Genus ***OVULASTER*** Cotteau, 1884

TYPE SPECIES

Ovulaster gauthieri Cotteau, 1884 (=*Cardiaster zignoi* d'Orbigny, 1854), by original designation.

DIAGNOSIS

Thick-shelled ovate test. Apical system ethmophract with four gonopores. Anterior ambulacrum weakly depressed on the upper surface and in a well defined groove close to the mouth. Paired ambulacra apetaloid or subpetaloid and virtually flush. Peristome facing downwards or obliquely forwards and at least 15% of test length from the anterior margin. Subanal fasciole present.

Ovulaster zignoi (d'Orbigny, 1854)

1854 *Cardiaster zignoi* d'Orbigny, p. 145; pl. 832: figs 8-13
1884 *Ovulaster gauthieri*; Cotteau p. 38; pl. 5: figs 1-3
?1940 *Ovulaster zignoi* (d'Orbigny); Rouchadzé p. 170
?1979 *Ovulaster zignoanus* (d'Orbigny); Gongadze, p. 121; pl. 27: fig. 3

DIAGNOSIS
Long wedge-shaped test with a subanal heel. Anterior ambulacrum in a well-defined groove on the lower surface. Rounded lower surface. Closely-spaced tuberculation on the upper surface.

OCCURRENCE
'Senonian' of Italy (d'Orbigny 1854) and possibly also the Maastrichtian of Georgia (Rouchadzé 1940; Gongadze 1979).

Ovulaster auberti Gauthier, 1892

1892 *Ovulaster auberti* Gauthier, p. 42; pl. 1: figs 3-9
1909 *Ovulaster auberti auberti* Gauthier; Blayac & Cottreau, p. 426; pl. 14: figs 1-3
1932 *Ovulaster auberti* Gauthier; Lambert, p. 76, 98
?1971 *Ovulaster* aff. *auberti* Gauthier; Akkus, p. 16

DIAGNOSIS
Globular test without a subanal heel. Anterior ambulacrum in a weak groove on the lower surface. Rounded lower surface. Mouth weakly angled forwards Widely-spaced tuberculation on the upper surface.

OCCURRENCE

This species, as well at *O. obtusus* has been reported from the Maastrichtian of Algeria and Tunisia. However, Zaghbib-Turki (1987) has reported that microfossils associated with both species are Coniacian in age, so a Coniacian age seems likely. Both species have also been reported from Turkey, but the Turkish specimens described by Akkus (1971) have not been seen as part of this study and the illustrations provided are not good enough to allow definitive assignment to *Ovulaster* species.

Ovulaster obtusus Cottreau in Blayac & Cottreau, 1909

1909 *Ovulaster obtusus* Cottreau in Blayac & Cottreau, p. 427; pl. 14: figs 20-28
1924 *Ovulaster truncatus* Lambert in Dalloni, p. 29
1932 *Ovulaster obtusus* Cottreau; Lambert, p. 77
?1971 *Ovulaster* aff. *obtusus* Cottreau; Akkus, p. 16

DIAGNOSIS

Short globular test without a subanal heel. Anterior ambulacrum in a well-defined groove on the lower surface. Rounded lower surface. Mouth points obliquely forward. Widely spaced tuberculation on the upper surface.

REMARKS

This species is very close to *O. auberti* but differs in having a shorter form, and in having a deeper and better-defined groove leading to the peristome that is more steeply angled forwards.

OCCURRENCE

See discussion of the occurrence of *O. auberti* and *O. obtusus* above. Probably Coniacian of Algeria and Tunisia (Zaghbib-Turki 1987); possibly also from the Maastrichtian of Turkey (Akkus 1971).

Ovulaster reticulatus Smith & Gallemí in Smith *et al.*, 1999

1999 *Ovulaster reticulatus* Smith & Gallemí in Smith *et al.*, p. 130; pl. 10; text-figs 39-40.

DIAGNOSIS

Ovate test with swollen ambulacral plates which are covered in a characteristic reticulate stereom meshwork. Anterior margin not cut by an anterior sulcus. Lower surface relatively flat. Aboral tubercules coarse and widely scattered.

REMARKS

O. reticulatus is distinguished from congeners on the basis of its swollen plates and characteristic reticulate stereom meshwork.

OCCURRENCE

Lower Maastrichtian of Navarra, Spain (Smith *et al.* 1999).

Genus ***PLESIASTER*** Pomel, 1883

TYPE SPECIES

Micraster peini Coquand, 1862, by original designation.

DIAGNOSIS

Test ovate with shallow anterior notch. Apical system ethmophract with four gonopores. Anterior ambulacrum subpetaloid and lying in a shallow groove. Paired ambulacra long (anteriors extend over 80% and posteriors over 60% of the distance to the ambitus), broad and sunken. Peristome greater than 15% of test length from anterior margin with opening clearly visible in oral view. Subanal fasciole present.

REMARKS

Smith & Jeffery (2000) placed a number of Maastrichtian species in the genus *Mokotibaster*. However, Smith (2005) pointed out that these species lack the marginal periproct and distinctive oral surface plating with three pairs of post sternal plates incorporated in the plastron that characterize *M. hourcqi*, the type species of *Mokotibaster* (which is probably a toxasterid). As a result, Smith suggests these species are better placed in *Plesiaster.* This position is followed here.

Plesiaster peini (Coquand, 1862)

Figure 2.5.1 A-B

1862 *Micraster peini* Coquand, p. 245; pl. 27: figs 1-3
1881 *Micraster peini* Coquand; Cotteau *et al.*, p. 55
1883 *Plesiaster peini* (Coquand); Pomel, p. 42
1889 *Micraster peini* Coquand; Gauthier, p. 27; pl. 2: fig. 3
1895 *Micraster peini* Coquand; Lambert, p. 247
1932 *Plesiaster peini* (Coquand); Lambert, p. 102
1975 *Micraster peini* Coquand; Stokes, p. 76; pl. 8: figs 1-5; text-fig. 30a

DIAGNOSIS

Test with a weak anterior notch and slightly overhanging posterior truncation. Anterior ambulacrum with round pores. Paired petals are very broad, the anterior pair reach approximately 85% of the distance to the ambitus and are roughly equal in length with the posterior pair. Peristome situated at around 20% of test length from the anterior margin; periproct situated at approximately 70% of the total test height from the base. Well developed subanal fasciole and traces of peripetalous fasciole at the petal ends.

OCCURRENCE

Santonian to Campanian of Algeria and Tunisia (Smith 2005).

Plesiaster amnicus (Greyling, 1996)

1990 *Hemiaster jacobi* Besairie & Lambert; Cooper & Greyling, p. 412; text-figs 2-6 (part)
1996 *Micraster amnicus* Greyling, p. 25; text-figs 2-7
2000 *Micraster (Mokotibaster) amnicus* (Greyling); Smith & Jeffery, p. 302

DIAGNOSIS
Test with shallow frontal notch and truncate posterior. Anterior ambulacrum with round pores. Paired petals broad and sunken, anterior pair reach approximately 80% of the distance to the ambitus. Sternal suture oblique. Peristome situated at approximately 20% of the test length from the anterior margin; periproct situated high on the posterior truncation. Subanal fasciole present.

OCCURRENCE
Early Maastrichtian of Zululand (Cooper & Greyling 1990; Greyling 1996); Late Maastrichtian of Tunisia (Smith & Jeffery 2000).

Plesiaster nobilis (Stoliczka, 1873)

1873 *Epiaster nobilis* Stoliczkca, p. 20; pl. 3: figs 7-8
1908 *Micraster* cf. *turonensis* Cottreau, p. 168; pl. 3: fig. 6
1930 *Epiaster nobilis* Stoliczka; Besairie, p. 231; pl. 24: fig. 8; pl. 25: fig. 3
1975 *Micraster nobilis* (Stoliczka); Stokes, p. 75; pl. 10: figs 3-6; text-fig. 29r (part)
2000 *Micraster (Mokotibaster) nobilis* (Stoliczka); Smith & Jeffery, p. 300-302; text-fig. 127a-c

DIAGNOSIS

Test with a shallow frontal groove and steeply overhanging posterior truncation; posterior forms a single point when viewed from above. Anterior ambulacrum with elongate pores. Paired petals are moderately broad, the anterior pair reach approximately 80% of the distance to the ambitus and are slightly longer than the posterior pair. The peristome is situated at 20% of the test length from the anterior margin; the periproct is situated at around 33% of the test height from the base. No fascioles are present.

REMARKS

Stokes (1975) included specimens of *Mokotibaster hourcqi* in this species. However, while *P. nobilis* has a fairly low periproct, *Mokotibaster* is considered distinct here due to its inframarginal periproct and characteristic plastron that incorporates three pairs of post sternal plates.

OCCURRENCE

Late Campanian to Maastrichtian of India (Stoliczka 1873) and Madagascar (Besairie 1930).

Plesiaster trangahyensis (Lambert, 1936)

?1908b *Epiaster* cf. *henrici* Peron & Gauthier; Cottreau, p. 163; pl. 3: fig. 9; text-fig. 10

1936 *Micraster trangahyensis* Lambert, p. 27; pl. 2: figs 9-10

2000 *Micraster (Mokotibaster) trangahyensis* (Lambert); Smith & Jeffery, p. 302; 127d-f

DIAGNOSIS

Test with shallow frontal notch and truncate posterior. Anterior ambulacrum with round pores. Paired petals broad and sunken, anterior pair reach approximately 65% of the distance to the ambitus. Sternal suture straight.

Peristome situated at approximately 20% of the test length from the anterior margin; periproct situated high on the posterior truncation. Subanal fasciole present.

OCCURRENCE

Early Maastrichtian of south-west Madagascar (Lambert 1936).

Genus ***TURANGLASTER*** Solovyev & Melikov, 1963

TYPE SPECIES

Turanglaster nazkii Solovyev & Melikov, 1963, by original designation.

DIAGNOSIS

Inflated ovate test with weak anterior notch and truncate posterior face. Apical system ethmophract with four gonopores. Anterior ambulacrum flush on upper surface but sunken on the oral surface. All ambulacra apetaloid. Periproct small and pentagonal and situated very close to the anterior margin, not covered by the labral plate. Periproct high on posterior face. Peripetalous fasciole present.

REMARKS

Turanglaster differs from *Ovulaster* primarily in the position of the peristome.

Turanglaster nazkii Solovyev & Melikov, 1963

1963 *Turanglaster nazkii* Solovyev & Melikov, p. 107; pl. 10: figs 1-2; text-fig. 1

DIAGNOSIS

As for genus.

OCCURRENCE

Campanian of Turkmenistan and Azerbaijan (Solovyev & Melikov 1963).

2.6 SUPERFAMILY PALEOPNEUSTOIDEA

Superfamily **PALEOPNEUSTOIDEA** Markov & Solovyev, 2001

DIAGNOSIS

Test cordate with petaloid paired ambulacra. Apical system ethmolytic or, rarely, semi-ethmolytic or ethmophract with two to four gonopores. Short, broad labrum followed by symmetrical sternal plates. Peripetalous fasciole always present, forming as a branch from an initial lateral fasciole; the latero-anal portion of this initial fasciole is usually present in adults.

REMARKS

Cretaceous paleopneustoids have historically been assigned to the Schizasteridae. This family has traditionally been defined by the presence of a latero-anal as well as a peripetalous fasciole. However, in some schizasterids the latero-anal fasciole, while always present in juveniles, may be lost in adults. Previous workers have considered the peripetalous fascioles of schizasterids and hemiasterids not to be homologous as the schizasterid peripetalous fasciole forms secondarily in development (e.g. Mortensen 1910; Néraudeau *et al.* 1998). However, Smith & Stockley (2005) have argued that hemiasterid & schizasterid peripetalous fascioles form at the same time and follow the same pathway as one another. They thus consider it likely that the structures are homologous with the fasciole that runs around the anterior of the schizasterid test representing a combined marginal-peripetalous fasciole. The diagnosis used here reflects the transitory nature of the latero-anal fasciole in some paleopneustids.

Smith & Stockley (2005) studied the course of fasciole bands over the test plating in spatangoid echinoids and showed that there are two distinct patterns for the combined marginal-peripetalous fasciole in taxa traditionally assigned to Schizasteridae. In the first pattern, which is exhibited by *Schizaster* (the type genus of the family Schizasteridae) the fasciole hugs the ends of the petals passing over plate 4 in interambulacra 2 and 3 and branches on plate 5 in columns 1b and 4a. In the second pattern, exhibited by taxa such as *Prenaster*, *Agassizia* and *Unifascia*, the fasciole passes well below the ends of the petals and crosses plate 3 in interambulacra 2 and 3 and branches on plate 4 in columns 1b and 4a (see Smith & Stockley (2005) for summary of plating terminology). Smith & Stockley (2005) suggested that the schizasterids could be separated into two distinct clades, Schizasteridae and Unifasciidae, on the basis of these fasciole pathways. This suggestion was supported by the phylogenetic analysis of Stockley *et al.* (2005), who termed the two clades Schizasteridae and Prenasteridae (the latter replacing the younger name Unifasciidae). These relationships are also recovered in the phylogenetic analysis of Cretaceous species presented here and this is reflected in the systematic palaeontology presented below. In the genus level phylogenetic analysis presented in Chapter 3 the Paleopneustoidea form a paraphyletic group. The name is retained here nevertheless, as I consider it premature to overhaul higher-level spatangoid systematics on the basis of a single analysis that does not have strong statistical support. The constituent clades Schizasteridae and Prenasteridae each form monophyletic groups in the genus level analysis of Chapter 3.

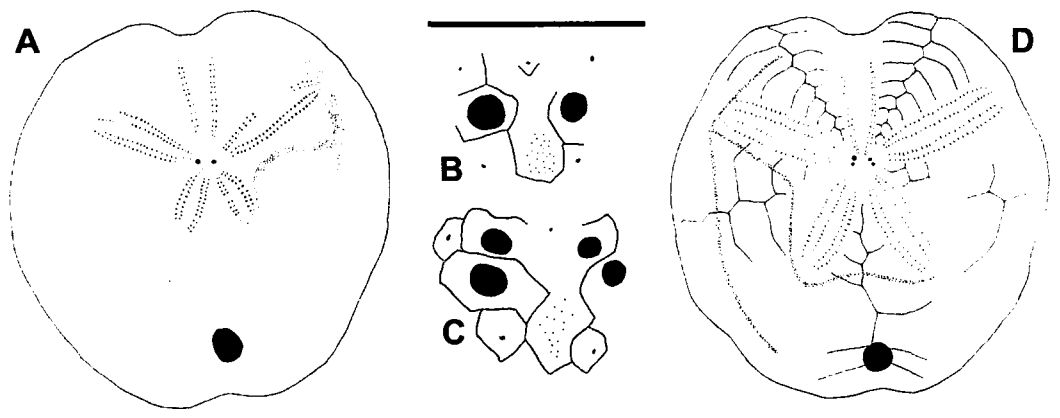

Figure 2.6.1: Schizasteridae. (**A-B**) *Abatus pseudoviviparus* MNHN J06016, Maastrichtian of Antonibe, north-west Madagascar, apical view and apical system; (**C-D**) *Schizaster sindensis* USNM 137371, Palaeocene of Alabama, USA, apical system and apical view. Relative scale bar: (A) 24.2 mm (B) 3.9 mm (C) 2.7 mm (D) 20.25.

KEY TO CRETACEOUS GENERA

1. Fasciole bounding the ends of the paired petals. Go to 2.

   Fasciole passing some distance below the ends of the anterior paired petals. Go to 6.

2. Two distinct fasciole bands around the test anterior. *Polydesmaster.*

   Single (combined) fasciole band around the test anterior. Go to 3.

3. Apical disc ethmophract or semi-ethmolytic. *Periaster.*

   Apical disc ethmolytic. Go to 4.

4. Posterior paired petals greater than 80% of the length of the anterior pair. *Linthia.*

   Posterior paired petals greater than 80% of the length of the anterior pair. Go to 5.

5. Lower surface with a series of prominent nodes adjacent to the plastron. *Tessieria.*

Lower surface without prominent nodes. *Schizaster.*

6. Test sloping very steeply at both anterior and posterior. *Holcopneustes.*

Test relatively gently sloping. *Lambertiaster.*

Stem-group **PALEOPNEUSTOIDEA** or stem-group **SCHIZASTERIDAE**

Genus ***POLYDESMASTER*** Lambert, 1920b

[=*Mundaster* Soares & Devriès, 1967, type species *Mundaster tentugalensis* Soares & Devriès, 1967]

TYPE SPECIES

Polydesmaster fourtaui Lambert, 1920b by original designation.

DIAGNOSIS

Paleopneustine spatangoid with semi-ethmolytic apical system, sub-equal paired petals, and marginal and peripetalous fascioles that do not merge anteriorly.

REMARKS

Smith (2005) in considered this taxon to be a stem group paleopneustid, as found in the phylogenetic analysis of Stockley *et al.* (2005). However, the phylogenetic analysis presented in Chapter 3 of this thesis suggests that this genus lies in the stem group of the schizasterids.

Polydesmaster fourtaui Lambert, 1920b

1920b *Polydesmaster fourtaui* Lambert, p. 23; pl. 2: figs 7-11.

DIAGNOSIS

Cordate test with sunken anterior ambulacrum and paired petals. Apex semi-ethmolytic, subcentral. Paired petals sub-equal in length; the anterior pair diverging at approximately 110°, the posterior pair at approximately 40°. Labral plate relatively long and flask-shaped.

OCCURRENCE

Cenomanian of Algeria (Lambert, 1920b).

REMARKS

Distinguished from *P. tentugalensis* by having less divergent anterior and posterior paired petals and a longer labral plate.

Polydesmaster tentugalensis (Soares & Devriès, 1967)

1967 *Mundaster tentugalensis* Soares & Devriès, p. 8-10; fig. 2; pl. 1: figs 1-9.

2001 *Mundaster tentagulensis* Soares & Devriès; Markov & Solovyev, pl. 4, text-fig. 12.

DIAGNOSIS

Cordate test with sunken anterior ambulacrum and paired petals. Apex semi-ethmolytic, subcentral. Paired petals sub-equal in length; the anterior pair diverging at approximately 140°, the posterior pair at approximately 50°. Labral plate short and T-shaped.

OCCURRENCE

Cenomanian – Turonian of Portugal (Soares & Devriès 1967).

Family **SCHIZASTERIDAE** Desor, 1853

DIAGNOSIS

Paleopneustid spatangoids with a sunken anterior ambulacrum with differentiated pore-pairs, unequal paired petals and a short T-shaped labral plate. A single fasciole passes around the anterior of the test, crossing plate 4 in interambulacra 2 and 3 and hugging the ends of the anterior paired petals before splitting into peripetalous and latero-anal branches on plate 5 in columns 1b and 4a.

REMARKS

I use the more restricted definition of Schizasteridae proposed by Smith (2005), which reflects the finding that the taxa previously assigned to this group form two clades with distinct fasciole pathways (Stockley *et al.* 2005).

Genus ***SCHIZASTER*** Agassiz, 1836

[=*Paraster* Pomel, 1869 type species *Schizaster gibberulus* Agassiz in Agassiz & Desor, 1847]

TYPE SPECIES

Schizaster studeri Agassiz 1836 by ICZN ruling 1948. (Eocene, Italy.)

DIAGNOSIS

Ovate test with prominent anterior groove and sunken paired petals, the posterior pair being less than 80% of the length of the anterior pair. Apical system ethmophract with four gonopores. Labral plate short and T-shaped. well developed peripetalous and latero-anal fascioles.

REMARKS

Mortensen separated schizasterids with unequal paired petals and well developed latero-anal fascioles bearing four gonopores into the genus *Paraster* and those bearing two gonopores into the genus *Schizaster.* This

was because he believed that the type species of *Paraster* (*P. gibberulus*, Recent) had four gonopores while the type species of *Schizaster* (*S. studeri*, Eocene) only had two. While the holotype of *P. gibberulus* does have four gonopores, the number in the holotype of *S. studeri* is unknown. Smith (2005) figured a well-preserved specimen of *S. studeri* from the type locality that clearly has four gonopores. He therefore synonymized the two genera into a single genus *Schizaster* containing the specimens with four gonopores, and placed those specimens with two gonopores in the genus *Ova* (which has no Cretaceous representatives and is not discussed further here). This position is followed here.

Schizaster chargensis (Wanner, 1902)

1902 *Hemiaster chargensis* Wanner, p. 108, pl. 15: figs 11-13
1914 *Linthia chargensis* (Wanner); Fourtau, p. 92, pl. 8: figs 6-9
1933 *Linthia paronai* Checchia-Rispoli, p. 11, pl. 1: figs 5-7
2000 *Paraster chargensis* (Wanner); Smith & Jeffery, p. 336

DIAGNOSIS
Low, flat-based test with highest point posterior, on sharp keel behind the apical system. Apical system at mid-length. Petals quite deeply sunken with the anterior pair around double the length of the posterior pair.

OCCURRENCE
Maastrichtian of Libya (Checchia-Rispoli 1933) and Egypt (Fourtau 1914). Also found in the Palaeocene of North Africa and, possibly, Australia (see Smith & Jeffery 2000).

REMARKS
Differs from *P. sindensis* and *P. variabilis* by having its high point more posteriorly positioned. Differs additionally from *P. sindensis* by having

proportionally shorter posterior paired petals and a sharper keel, and from *P. variabilis* in lacking the pustular tuberculation and sharp keels in all interambulacra characteristic of that species. Differs from *P. indicus* in having a flat base.

Schizaster indicus (Duncan & Sladen, 1882b)

1882b *Linthia indica* Duncan & Sladen, p. 82, pl. 20: figs 1-8
1933a *Periaster inconstans* Lambert, p. 25, pl. 4: fig. 15
1979 *Linthia inconstans* (Lambert); Tanaka *et al.* p. 39, pl. 2: figs 4a-d, 5a-d; pl. 3: fig. 1; text-fig. 11a-c
1979 *Linthia (Linthia) madagascariensis* Tanaka *et al.*, p. 41, pl. 3: figs 2 a-d, 3, 4; text-fig. 12a-c
2000 *Paraster indicus* (Duncan & Sladen); Smith & Jeffery, p. 337-338; text-fig. 138.

DIAGNOSIS
Circular to hexagonal test with highest point posterior. Apical system at mid-length. Paired petals sunken; anterior paired petals twice as long as posterior pair. Lower surface inflated.

OCCURRENCE
Maastrichtian to Danian of Madagascar (Lambert 1933a; Besairie 1971; Tanaka *et al.* 1979). Also found in the Palaeocene of Pakistan, Senegal and the Ivory Coast (see Smith & Jeffery 2000).

Schizaster joannisboehmi (Oppenheim in Böhm, 1903)

1903 *Linthia*(?) *joannis böhmi* Oppenheim in Böhm, 1903 p. 72
2005 *Paraster joannisboehmi* (Oppenheim in Böhm, 1903); Parma & Casadío, p. 1081, text-figs 13.1-13.4, 14.

DIAGNOSIS

Globular, circular to hexagonal test with moderate anterior groove and inflated lower surface. Highest point on relatively sharp keel a short distance behind apical system. Apical system ethmolytic with four gonopores, central. Anterior paired petals approximately twice as long as posterior pair.

OCCURRENCE

Upper Maastrichtian to Upper Danian of Argentina (Parma & Casadío 2005).

REMARKS

Close to *P. indicus* but differs in having its highest point more central, less sunken petals and a sharper posterior keel.

Schizaster sindensis (Duncan & Sladen, 1882a)

Figure 2.6.1 C-D

1882a *Linthia sindensis* Duncan & Sladen, p. 18: pl. 4
1933a *Linthia sindensis* Duncan & Sladen; Lambert, p. 26, pl. 4: fig. 16
1994 *Linthia bajsarensis* Markov, p. 58, pl. 1: fig. 3; pl. 2: figs 1-3; text-figs 15-16
1994 *Linthia spiennensis* Schlüter; Markov, p. 56, pl. 1: fig. 1; text-fig. 15
2000 *Paraster sindensis* (Duncan & Sladen); Smith & Jeffery, p. 336

DIAGNOSIS

Low test with flat base and highest point central. Upper surface with no keels. Apical system at mid-length. Anterior paired petals approximately 1.5 times longer than posterior pair.

OCCURRENCE

Late Maastrichtian of Turkmenistan (Markov 1994). Also from the Palaeocene of India, Madagascar, USA, Transcaspian region, Belgium and the Netherlands (see Smith & Jeffery 2000).

Schizaster variabilis (Slocum, 1909)

1909 *Linthia variabilis* Slocum, p. 12, pl. 3: fig. 1; text-fig. 1
1915 *Linthia variabilis* Slocum; Clark & Twitchell, p. 99, pl. 54: fig. 1
1941 *Linthia variabilis* Slocum; Stephenson, p. 68, pl. 8, figs 1-5
1953 *Linthia variabilis* Slocum; Cooke, p. 36, pl. 14: figs 18-25
2000 *Paraster variabilis* (Slocum); Smith & Jeffery, p. 337

DIAGNOSIS

Test with flat base and highest point central. Apical system at mid-length. Deeply sunken paired petals with sharply keeled interambulacra. Anterior paired petals approximately double the length of the posterior pair. Pustular tuberculation on apical surface.

OCCURRENCE

Late Campanian and Maastrichtian of Mississippi, North Carolina, Texas and Arkansas, USA (Cooke 1953).

REMARKS

Distinguished by its pustular tuberculation and deeply sunken petals with sharply keeled interambulacra between.

Genus ***ABATUS*** Troschel, 1851

TYPE SPECIES

Spatangus (Tripylus) cavernosus Philippi, 1845 by original designation. (Recent, South America and Antarctica.)

DIAGNOSIS

Cordate test with distinct frontal groove. Anterior ambulacrum subpetaloid. Paired petals broad and deep; anterior pair somewhat flexuous distally. Apical system ethmolytic with two or three gonopores. Peripetalous fasciole bounding the ends of the petals; with or without latero-anal fasciole in adults.

REMARKS

Abatus is most similar to *Tripylus*, but is traditionally distinguished by having a peripetalous fasciole that bounds the petals (rather than passing two to three plates below). It has also been traditionally thought to have a more distinct frontal groove and no latero-anal fasciole in adults. In addition, Mortensen has argued that *Tripylus* always has three gonopores (rather than two) in its apical system. However, while the Cretaceous specimens described below have two gonopores, a deep frontal notch and petals bound by the peripetalous fasciole, they also show remnants of a latero-anal fasciole in adult material; the fasciole is at least patially present at 27 mm, whereas the latero-anal fasciole is lost at only a few millimetres in the Recent species. This leads me to re-diagnose the genus to include those forms with a latero-anal fasciole in adult specimens.

Abatus pseudoviviparus (Lambert, 1933a)

Figure 2.6.1 A-B

1933a *Tripylus pseudoviviparus* Lambert, p. 27, pl. 4: figs 1-7
1933a *Tripylus antonibensis* Lambert, p. 28, pl. 4: figs 12-14
2000 *Abatus? pseudoviviparus* (Lambert); Smith & Jeffery, p. 351

DIAGNOSIS

Test with depressed frontal groove. Apical system with two gonopores. Peripetalous fasciole bounds petals; latero-anal fasciole at least partially present.

OCCURRENCE

Maastrichtian of north-west Madagascar (Lambert 1933a). (Also found in the Palaeocene of Madagascar).

Genus ***LINTHIA*** Desor, 1853

[=*Lutetiaster* Lambert, 1920b, type species *Spatangus subglobosus* Lamarck, 1816]

TYPE SPECIES

Linthia insignis Merian in Desor, 1853 by original designation. (Eocene, France.)

DIAGNOSIS

Test ovate or cordiform with strong frontal groove and truncate posterior. Apical system ethmolytic with four gonopores. Paired petals long and straight; anterior and posterior pair subequal in length. Peripetalous fasciole deeply indented between petals; lateroanal fasciole also present.

REMARKS

Linthia differs from *Schizaster* in having posterior paired petals of at least 80% the length of the anterior paired petals. It differs from *Periaster* in having an ethmolytic, rather than ethmophract, apical system.

Linthia brodermanni Sánchez Roig, 1949

1949 *Linthia brodermanni* Sánchez Roig, p. 263, pl. 49: figs 2-4

?1949 *Linthia alta* Sánchez Roig, p. 266, pl. 49: figs 3-5

1949 *Hemiaster lamberti* Sánchez Roig, p. 238, pl. 35: figs 7-8

1949 *Micraster elevatus* Sánchez Roig, p. 218, pl. 47: figs 4-5

?1952 *Linthia gonzalezmunozi* Sánchez Roig, p. 23, pl. 9: fig. 1

1984 *Linthia brodermanni* Sánchez Roig; Kier, p. 73, pls 37-39; text-figs 27-28

2000 *Linthia brodermanni* Sánchez Roig; Smith & Jeffery, p. 334

DIAGNOSIS

Relatively elongate test with highest point central and apical system anterior. Parallel sided frontal groove. Petals slightly sunken with the posterior pair almost as long as the anterior.

OCCURRENCE

Late Cretaceous of Cuba (Kier 1984). (Also found in the Palaeocene of Senegal (Tessier 1952)).

REMARKS

The types *L. alta* and *L. gonzalezmunozi* are both very similar to that *L. brodermanni*, differing respectively only in having a higher test and a slightly narrower test with a slightly shallower anterior groove. Each of these species is known only from a single specimen meaning that it is difficult to assess the importance of these minor differences. As a result I tentatively treat both of these species as synonyms of *L. brodermanni*.

Linthia payeni (Coquand, 1880)

1880 *Hemiaster payeni* Coquand, p. 260

1881 *Linthia payeni* (Coquand); Cotteau *et al.*, p. 134, 151; pl. 12: figs 3-8

1881 *Hemiaster medjesensis* Peron & Gauthier in Cotteau *et al.*, p. 129; pl. 12: figs 1-2

1932 *Linthia payeni* (Coquand); Lambert, p. 150

1932 *Linthia medjesensis* (Peron & Gauthier); Lambert, p. 150

1935a *Linthia payeni* (Coquand); Lambert, p. 363

1939 *Linthia payeni* (Coquand); Airaghi, p. 265

1983 *Linthia payeni* (Coquand); Roman & Sornay, p. 14, pl. 1: figs 5-7

2000 *Linthia payeni* (Coquand); Smith & Jeffery, p. 332-333

DIAGNOSIS

Test with distinct carina in posterior interambulacrum. Anterior ambulacrum broad and depressed at apex, adjacent interambulacra form pinched keels. Paired petals broad and sunken with anterior and posterior pairs approximately equal in length.

OCCURRENCE

Campanian to Early Maastrichtian of Algeria (Cotteau *et al.* 1881), Campanian of Senegal (Roman & Sornay 1983), Mid-Late Maastrichtian of Libya (Airaghi 1939).

REMARKS

The characteristic pinched keels make this species easy to distinguish from its congeners. Peron & Gauthier (1881) described *Hemiaster medjesensis* for a single large specimen, which differed from *L. payeni* in having relatively longer posterior paired petals. Lambert transferred the species to *Linthia* and noted that it also had a sinuous peripetalous fasciole. Examination of specimens of both species in the MNHN, Paris, suggests that there is a continuous gradation between the two; they are thus considered here to be synonyms.

Linthia sudanensis (Bather, 1904)

1904 *Hemiaster sudanensis* Bather, p. 299, pl. 11: figs: 6-13

?1995 ?*Linthia sudanensis* (Bather); Smith p. 236, pl. 33: figs 3-9; text-figs 84B, 85

2000 *Linthia sudanensis* (Bather); Smith & Jeffery, p. 333; text-fig. 137.

DIAGNOSIS

Elongate test with an anterior groove that is flush close to the apex and deepens to the ambitus. Paired petals long, straight and only weakly sunken. Large tubercles along edges of frontal groove.

OCCURRENCE

?Late Campanian to Maastrichtian of the United Arab Emirates (Smith 1995). (Common in the Palaeocene of North Africa).

REMARKS

Linthia sudanensis is well known from the Palaeocene. One specimen from the Cretaceous of the United Arab Emirates is indistinguishable from *L. sudanensis*, but is too poorly preserved to be definitively assigned to this species.

Genus ***PERIASTER*** d'Orbigny, 1853

TYPE SPECIES

Periaster elatus d'Orbigny, 1853 [*Spatangus elatus* des Moulins, 1837] by subsequent designation of Lambert, 1918.

DIAGNOSIS

Ovate test with distinct anterior sulcus. Apical system central; ethmophract or semi-ethmolytic with four gonopores. Posterior paired petals shorter than anterior pair. Peripetalous fasciole bounds petals and is indented at the anterior, behind the anterior paired petals and in the posterior interambulacrum; lateroanal fasciole also present.

REMARKS

The genus *Periaster* has been used in two ways in the literature. Firstly, for those species close to the type species, *P. elatus*, and secondly, for species of *Mecaster* or *Hemiaster* which have developed a latero-anal fasciole. The former are generally considered to be true schizasterids, while the latter are not and Lambert (1932) proposed that these specimens should be termed the *bifasciata* stage or variety of the hemiasterid species in question. I excluded hemiasterid taxa at the *bifasciata* stage from this study using the following criteria to identify them: (1) a long triangular labral plate; (2) paired petals approximately equal in length; (3) anterior groove not significantly shallower than paired petals; and (4) peripetalous fasciole not deeply indented between paired petals. It should be noted, however, that more work is required in order to elucidate the phylogenetic relationships of these species and their relationships to "true" schizasterids. *Periaster* is distinguished from *Linthia* by having an ethmophract or semi-ethmolytic, rather than ethmolytic, apical system.

Periaster elatus (des Moulins, 1837)

1837 *Spatangus elatus* des Moulins, p. 406
1853 *Periaster elatus* (des Moulins); d'Orbigny, p. 270, pl. 897

DIAGNOSIS

High test with posterior face vertical in upper part, but oblique in lower. Anterior ambulacrum weakly depressed close to the apex, but becomes flush before the ambitus. Anterior paired petals diverge at approximately 120° and are around 1.4 times longer than the posterior pair, which diverge at about 80°. Apical system at mid-length; ethmophract with four gonopores.

OCCURRENCE

Cenomanian of SW France (Néraudeau *et al.* 2003).

REMARKS

Distinguished from all other schizasterids by having a fully ethmophract apical system.

Periaster ciryi Lambert, 1935c

1935c *Periaster ciryi* Lambert, p. 520, pl. 57: figs 13-15

DIAGNOSIS

Wedge shaped test with the highest point posterior and a vertical posterior face. Apical sytem at mid-length; semi-ethmolytic with four gonopores. Anterior ambulacrum in a broad, shallow groove. Paired petals depressed, the anterior pair diverge at approximately 115° and are around 1.3 times the length of the posterior pair, which diverge at approximately 80°.

OCCURRENCE

Coniacian of Becerril del Carpio, Spain (Lambert 1935c).

Periaster undulatus (Agassiz, 1847)

1847 *Micraster undulatus* Agassiz in Agassiz & Desor, p. 130
1854 *Periaster undulatus* (Agassiz); d'Orbigny, p. 272, pl. 898
1869 *Periaster undulatus* (Agassiz); Cotteau & Triger p. 214 pl. 24 fig. 10-11

DIAGNOSIS

Relatively high test with a high vertical posterior face. Narrow and strongly depressed paired petals, but anterior ambulacrum only weakly depressed. Anterior paired petals diverge at approximately 110°, the posterior pair

diverge at approximately 70° and are only slightly shorter than the anterior pair.

OCCURRENCE

Cenomanian of Charantes, southwest France (Néraudeau *et al.* 2003).

Genus ***TESSIERIA*** Collignon, 1949

TYPE SPECIES

Tesseria senegalensis Collignon, 1949, by original designation.

DIAGNOSIS

Inflated upper surface. Large nodules on the ambulacral plates bordering the plastron (four nodules on each side). Paired ambulacra forming deeply sunken petals; anterior pair reach ambitus in plan view. Apical system ethmolytic with four gonopores. Peripetalous fasciole bounds the petals and is strongly indented behind the anterior paired petals; lateroanal fasciole also present.

REMARKS

Easily distinguished from all other Cretaceous schizasterids by the presence of large nodules on the ambulacra adjacent to the plastron.

Tessieria senegalensis Collignon, 1949

1949 *Tessieria senegalensis* Collignon, p. 263, pl. 9a: figs 1-5; text-figs 1-2.

1952 *Tessieria senegalensis* Collignon; Tessier, p. 307; pl. 18: figs 19-20.

2000 *Tessieria senegalensis* Collignon; Smith & Jeffery, p. 339-340; text-fig. 139

DIAGNOSIS

As for genus.

OCCURRENCE

Late Maastrichtian of Senegal (Tessier 1952).

Family **PRENASTERIDAE** Lambert, 1905

[=Unifasciidae Cooke, 1959]

DIAGNOSIS

Paleopneustine spatangoids with an anterior ambulacrum with undifferentiated pore-pairs, unequal paired petals and a short T-shaped labral plate. A single fasciole passes around the anterior of the test, crossing plate 3 in interambulacra 2 and 3. Fasciole then passes several plates from the ends of the anterior paired petals before splitting into peripetalous and latero-anal branches on plate 4 in columns 1b and 4a.

REMARKS

The following genera are most likely to belong to this family, though their exact fasciole pathways have not been determined.

Genus ***HOLCOPNEUSTES*** Cotteau, 1889b

TYPE SPECIES

Holcopneustes gourdoni Cotteau, 1889b by original designation. (Eocene, Spain).

DIAGNOSIS

Test angular in outline with distinct anterior sulcus; widest at mid-length. Narrow frontal groove extending from apex to peristome. Petals long and deeply sunken; anterior and posterior pair subequal in length; anterior pair

somewhat flexuous. Apical system at 30-40% of test length from anterior; ethmolytic with four gonopores. Labral plate relatively long. Peripetalous fasciole passes some distance below the ends of the petals; not strongly indented behind the anterior paired petals; no latero-anal fasciole.

REMARKS

Differs from *Lambertiaster* in having a test that is vertically truncate at anterior and posterior; differs from *Mauritanaster* in having a more inflated test with more deeply sunken petals.

Holcopneustes cristatus (Stoliczka, 1873)

1873 *Hemiaster cristatus* Stoliczka, p. 17, pl. 3: figs 2-5
1933a *Holcopneustes narindensis* Lambert, p. 24, pl. 4: figs 8-10
1973 *Holcopneustes ghiroboensis* Tessier & Roman, p. 157, pl. 2: figs 4-7
2000 *Holcopneustes cristatus* (Stoliczka); Smith & Jeffery, p. 345; text-fig. 141a-c

DIAGNOSIS

Test subconical in profile with a flat base. Anterior petals diverge at 120-150° and reach approximately 75% of the distance to the ambitus. Posterior paired petals diverge at 25-55° and reach approximately 50% of the distance to the ambitus. Apical system at 20-30% of test length from the anterior.

OCCURRENCE

Maastrichtian of southern India (Stoliczka 1873). Also known from the Palaeocene of Madagascar (Lambert 1933a) and the Ivory Coast (Tessier & Roman 1973).

Holcopneustes indicus (Stoliczka, 1873)

1873 *Hemiaster indicus* Stoliczka, p. 16, pl. 2: figs 6-7; pl. 3: fig. 1

1873 *Hemiaster rana* Stoliczka, p. 15, pl. 2: figs 4-5

1873 *Hemiaster tuberosus* Stoliczka, p. 12, pl. 1: figs 3-6

1873 *Hemiaster pullus* Stoliczka, p. 18, pl. 2: figs 8-9

1882b *Linthia* sp. Duncan & Sladen, p. 85, pl. 20: fig. 5

1897 *Hemiaster pullus* Stoliczka; Kossmat, pp. 61, 96, pl. 10: fig. 6

1897 *Hemiaster blanfordi* Noetling, p. 35, pl. 8: fig. 3

1908b *Hemiaster boulei* Cottreau, p. 171, pl. 3: fig. 8; text-fig. 14

1930 *Mecaster (Hemiaster) cristatus* (Stoliczka); Besairie, p. 231, pl. 23: fig. 9

2000 *Holcopneustes indicus* (Stoliczka); Smith & Jeffery, p. 345

DIAGNOSIS

Test domed in profile with rounded base. Very sharp keel running from apex to periproct. Anterior petals diverge at 95-155° and extend approximately 85% of the distance to the ambitus. Posterior petals at 35-70° and extend approximately 65% of the distance to the ambitus. Apical sytem at approximately 40% of test length.

OCCURRENCE

Late Maastrichtian of southern India (Stoliczka 1873); Maastrichtian of Baluchistan (Noetling 1897) and northwest Madagascar (Besairie 1930). [Also from the Palaeocene of Pakistan (Duncan & Sladen 1882b) and Madagascar (Besairie 1971).]

REMARKS

Very similar to *H. cristatus* but differs in having a domed profile and rounded base, petals that are longer with the anterior pair being less divergent and a more posterior apical system.

Genus ***LAMBERTIASTER*** Gauthier, 1892

TYPE SPECIES

Lambertiaster douvillei Gauthier, 1892 by original designation.

DIAGNOSIS

Test domed with rounded outline and shallow anterior sulcus. Apical disc central with four gonopores. Peripetalous fasciole passes some distance below the ends of the petals; no latero-anal fasciole.

REMARKS

While the genus level phylogeny presented in Chapter 4 groups *Lambertiaster* with *Holcopneustes*, *Lambertiaster* also resembles *Homoeaster*, differing in having more sunken petals and a fasciole that passes well below the ends of the paired petals. The fasciole can also pass below the paired petals in *Homoeaster*, but the pathway the fasciole follows over the plates of the test differs between aeropsids and prenasterids (see Smith & Stockley, 2005). Unfortunately, none of the *Lambertiaster* material studied was sufficiently well preserved to determine the fasciole pathway. As a result this genus is provisionally assigned to the prenasterids pending future study.

Lambertiaster douvillei Gauthier, 1892

1892 *Lambertiaster douvillei* Gauthier, p. 30; pl. 3: figs 1-3

?1924 *Lambertiaster fischeri* Dalloni & Lambert in Dalloni, p. 474; pl. 12: figs 3-5

1932 *Lambertiaster douvillei* Gauthier; Lambert p. 77,112

DIAGNOSIS

As for genus.

OCCURRENCE

Campanian – Maastrichtian of Tunisia (Gauthier 1892); Maastrichtian of Algeria (Dalloni & Lambert in Dalloni 1924).

2.7 FAMILY SOMALIASTERIDAE

The atelostomate family Somaliasteridae was erected by Wagner & Durham (1966) for the genera *Iraniaster* Cotteau & Gauthier, 1895, *Somaliaster* Hawkins, 1935, *Brightonia* Kier, 1957 and *Leviechinus* Kier, 1957. These taxa have been discussed and figured by Kier (1957, 1972), who also synonymized *Iraniaster* and *Somaliaster* (Kier 1972). The phylogenetic position of the family within atelostomates has been problematic because the included taxa share not only a compact apical system and depressed petals (typical of spatangoids), but also a meridosternous plastron (typical of holasteroids). Authors have variously assigned somaliasterid taxa to both groups (see table 1 of Jeffery 1999). Jeffery (1999) used phylogenetic analysis to determine the position of somaliasterids within the atelostomates, concluding that they are in fact spatangoids. Jeffery (1999) also presented diagnoses for the various somaliasterid taxa and the taxonomic scheme presented here largely follows that of Jeffery.

Family **SOMALIASTERIDAE** Wagner & Durham, 1966

DIAGNOSIS

Paired ambulacra form long petals with large numbers of pores. Plastron meridosternous but approaches the amphisternous condition. Labral and sternal plates may be disjunct. Apical system compact and may be ethmolytic, semi-ethmolytic or ethmophract. Peripetalous fasciole present.

REMARKS

Easily distinguished from other spatangoids with only peripetalous fascioles by their plastron plating which is meridosternous but approaches an amphisternous condition. The somaliasterids have previously been placed in the holasteroids, but Jeffery (1999) used a phylogenetic analysis to demonstrate that they are, in fact, spatangoids.

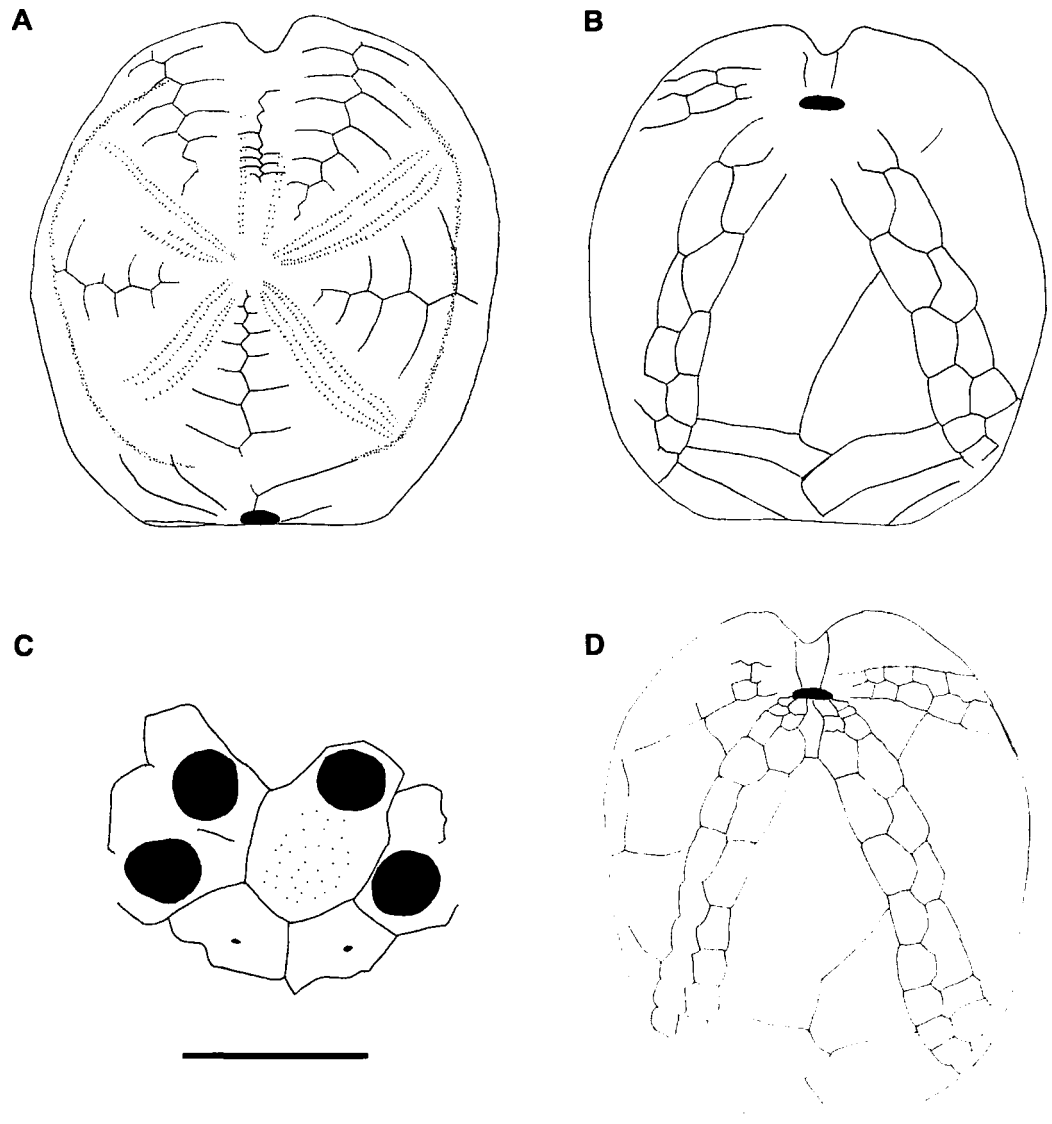

Figure 2.7.1: Somaliasteridae. (**A-B**) *Iraniaster affinimorgani* holotype, USNM 170462, Campanian Aruma Formation of northern Tuwayq, Saudi Arabia, apical and oral views; (**C-D**) *Iraniaster bowersi* paratype, USNM 170506, Campanian Aruma Formation of Northern Tuwayq, Saudi Arabia, apical system and oral view. Relative scale bar: (A) 18.0 mm (B) 18.0 mm (C) 1.9 mm (D) 22.7 mm.

Genus ***IRANIASTER*** Cotteau & Gauthier, 1895

[=*Somaliaster* Hawkins, 1935, type species *Somaliaster magniventer* Hawkins, 1935]

TYPE SPECIES

Iraniaster morgani Cotteau & Gauthier, 1895, by original designation.

DIAGNOSIS

Widest point at mid-length. Apical system semi-ethmolytic or ethmolytic with four gonopores. Petals only slightly depressed. Plastron meridosternous, sometimes disjunct.

REMARKS

Kier (1972) synonymized *Somaliaster* with *Iraniaster*, recognizing *Somaliaster magniventer* as a junior synonym of *Iraniaster douvillei*. This was followed by Jeffery (1999) and Smith & Jeffery (2000), but Smith (2005) argued that *Somaliaster* can be separated on the basis of its non-disjunct plastron. However, non-disjunct plastrons are also observed in *I. bowersi*, *I. affinidouvillei* and *I. affinimorgani*, even in large (>35 mm) specimens. I therefore follow Kier (1972) and place *Somaliaster* in synonomy. *Iraniaster* differs from the Palaeocene genera *Leviechinus* and *Brightonia* in having four gonopores in the apical system, rather than two.

KEY TO CRETACEOUS SPECIES

1. Ethmolytic apical system. *Iraniaster omanensis.*
   Semi-ethmolytic apical system. Go to 2.

2. Labral and sternal plates disjunct in specimens greater than 35 mm in length. *Iraniaster morgani.*
   Labral and sternal plates in contact. Go to 3.

3. Periproct low on posterior face; flush or gently sunken anterior groove and paired petals. Go to 4.
   Periproct high on posterior face; anterior groove and paired petals sunken. Go to 5.

4. Paired petals practically flush. *Iraniaster douvillei.*

Paired petals gently sunken; peristome approximately 10% of test length from the anterior margin. *Iraniaster affinidouvillei.*

5. Test approximately as long as wide. *Iraniaster affinimorgani.*

Test markedly longer than wide. *Iraniaster bowersi.*

Iraniaster morgani Cotteau & Gauthier, 1895

1895 *Iraniaster morgani* Cotteau & Gauthier, p. 28, pl. 4, figs 1-12

2000 *Iraniaster morgani* Cotteau & Gauthier; Smith & Jeffery, p. 362-363; text-fig. 150

DIAGNOSIS

Distinct frontal notch. Anterior right of test projects beyond left. Low domed upper surface and slightly convex lower surface. Paired ambulacra form virtually flush petals with equally elongate pores; anterior petals diverge at 100 degrees, posterior petals at 75 degrees. Plastron meridosternous (approaching amphisternous) with labral and sternal plates disjunct in larger specimens (> about 35 mm test length). Two post sternal plates approximately equal in size and symmetrically placed. Apical system semi-ethmolytic with four gonopores. Narrow peripetalous fasciole not indented between petals.

OCCURRENCE

Senonian (Campanian to Maastrichtian) of Iran (Cotteau & Gauthier 1895).

Iraniaster affinidouvillei Kier, 1972

1972 *Iraniaster affinidouvillei* Kier, p. 74, pl. 52, figs 4-7; pl. 53; text-figs 37d, 39d, 44

DIAGNOSIS

High smooth test with a shallow anterior notch extending to the peristome. Apical system central to slightly posterior, semi-ethmolytic with four gonopores. Anterior ambulacrum weakly depressed, not petaloid and with large pore-pairs; paired petals long and shallow. Plastron not disjunct.

REMARKS

The petals and anterior notch are deeper than those of *I. douvillei* yet shallower than those of *I. affinimorgani.*

OCCURRENCE

Campanian Lower Aruma Formation of Saudi Arabia, between 78 and 85 km markers on the Khurais-Riyadh road (Kier 1972). Campanian of Nafun, near Duqm, Oman (BMNH).

Iraniaster affinimorgani Kier, 1972

Figure 2.7.1 A-B

1972 *Iraniaster affinimorgani* Kier, p. 77, pl. 51; pl. 52 figs 1-3; text-figs 37d, 39d, 44

DIAGNOSIS

Low angular test, with deep anterior groove. Apical system central, semi-ethmolytic with four gonopores. Paired petals deep; anterior pair only just longer than posterior.

REMARKS

The depth of the anterior notch and paired petals distinguish *I. affinimorgani* from all congeners other than *I. bowersi*, from which it differs in having a higher and wider test, a shorter plastron, a deeper anterior ambulacrum adapically and larger pore-pairs in the anterior ambulacrum.

OCCURRENCE

Campanian Lower Aruma Formation of Saudi Arabia, between 78 and 85 km markers on the Khurais-Riyadh road (Kier 1972).

Iraniaster bowersi Kier, 1972

Figure 2.7.1 C-D

1972 *Iraniaster bowersi* Kier, p. 81, pl. 54; text-figs 38b, 40

DIAGNOSIS

Low, narrow test with distinct anterior notch. Apical system posterior of centre, semi-ethmolytic with four gonopores. Anterior ambulacrum slightly sunken near apical system, but forming a deep groove at the ambitus. Plastron long.

REMARKS

Most similar to *I. affinimorgani* but distinguished by having a longer, narrower test, longer plastron, shallower anterior ambulacrum near the apex and smaller pore-pairs in the anterior ambulacrum between the apical system and peripetalous fasciole.

OCCURRENCE

Campanian Lower Aruma Formation of Saudi Arabia (several localities, see Kier (1972) for details).

Iraniaster douvillei Cotteau & Gauthier, 1895

1895 *Iraniaster douvillei* Cotteau & Gauthier, p. 30, pl. 5, figs 1-6
1935 *Somaliaster magniventer* Hawkins, p. 53, pl. 7, figs 2-3; text-figs 1-3
1941 *Somaliaster magniventer* Hawkins; Maccagno, p. 89, pl. 11, figs 1-9, 12; text-figs 1-3
1941 *Somaliaster magniventer* var. *checchiai* Maccagno, p. 93, pl. 11, figs 10-11
1954 *Somaliaster magniventer* Hawkins; Joysey, p. 45, text-fig. 1
2000 *Iraniaster douvillei* Cotteau & Gauthier; Smith & Jeffery, p. 363-364; text-fig. 151

DIAGNOSIS

Relatively high test with somewhat gibbous profile and shallow frontal groove. Paired petals weakly sunken; anterior paired petals diverge at 110-120 degrees; posterior pair diverge at 85-90 degrees. Plastron not disjunct. Peristome anteriorly positioned: at approximately 10% of test length from the anterior margin.

REMARKS

Differs from *I. morgani* in having a higher, more gibbous profile; shallower frontal groove; non-disjunct plastron even in large specimens; anterior and posterior petals more widely divergent; less distinct peripetalous fasciole. Differs from *I. affindouvillei* in having more sunken paired petals and anterior groove and a more anteriorly positioned mouth.

OCCURRENCE

Senonian (Campanian to Maastrichtian) of Iran (Cotteau & Gauthier 1895) and Maastrichtian of Somalia (Hawkins 1935; Maccagno 1941); Santonian to Campanian of Oman (MNHN).

Iraniaster omanensis Jeffery, 1999

1999 *Iraniaster omanensis* Jeffery, p. 1032, pl. 1, figs 6-8, text-fig. 4
2000 *Iraniaster omanensis* Jeffery; Smith & Jeffery, p. 365

DIAGNOSIS
Weakly cordate test with broad, shallow frontal groove. Paired ambulacra form long, straight, sunken petals; anterior paired petals diverge at 140 degrees, posterior pair at 60 degrees. Apical system ethmolytic with four gonopores. Plastron meridosternous with labral and sternal plates disjunct. Narrow peripetalous fasciole not indented between paired petals.

REMARKS
Most similar to *Iraniaster douvillei*, but can be distinguished by its more divergent anterior petals, less divergent posterior petals, and more anterior apical system. It is unique among *Iraniaster* species in having a fully ethmolytic apical system, but as Jeffery (1999) points out this could be a function of the large size of the available specimens. In the phylogenetic analysis presented in this thesis this species falls outside the well-supported clade containing the other species assigned to *Iraniaster*. It lies at the base of a clade containing the two Palaeocene somaliasterid genera *Brightonia* and *Leviechinus*. However, as this clade is not strongly supported and as a monophyletic *Iraniaster* clade is not a significantly worse explanation of the data (see section 3.8.4), this species is retained in the genus *Iraniaster*.

OCCURRENCE
Maastrichtian Simsima Formation of Jebel Lahjan, 8 km southeast of Yanqul, Oman (Jeffery 1999).

2.8 FAMILY UNCERTAIN

The following spatangoids are too poorly known to be confidently placed in one of the spatangoid families.

Genus ***BARNUMIA*** Cooke, 1953

TYPE SPECIES

Barnumia browni Cooke, 1953 by original designation.

REMARKS

Barnumia Cooke, 1953 is based on a single species, *B. browni*, which most likely originates from the Campanian of Guatemala. Smith (2005) placed this species within the genus *Homoeaster*. While it is possible that *B. browni* belongs in this genus, because the lower surface is not preserved and the species has relatively well developed petals with the fasciole passing some distance from the petal terminations, it is also possible that it is a prenasterid. I take a conservative approach and consider the higher taxonomy of this species to be unknown pending the discovery of specimens preserving the oral surface.

Barnumia browni Cooke, 1953

1953 *Barnumia browni* Cooke, p, 30; pl. 16: figs 2-5

Genus **GREGORYASTER** Lambert, 1907

TYPE SPECIES

Pericosmus coranguinum Gregory, 1892, by original designation (Miocene of the Mediterranean).

REMARKS

This genus resembles *Hemiaster* but differs in having long narrow petals. The type species has traces of a marginal fasciole, which has not been observed in Cretaceous material, meaning their assignment to this genus is uncertain.

Gregoryaster jacobi (Besairie & Lambert, 1930)

1930 *Hemiaster jacobi* Besairie & Lambert, p. 109; pl. 9: figs 2-3
1933a *Hemiaster narindensis* Lambert, p. 24; text-fig. 2
1990 *Hemiaster jacobi* Besairie & Lambert; Cooper & Greyling, p. 412; text-fig. 2
2000 *Gregoryaster jacobi* (Besairie & Lambert); Smith & Jeffery, p. 331

Genus **TRACHYASTER** Pomel, 1869

TYPE SPECIES
Trachyaster globosus Pomel, 1869 by original designation (Pliocene of the Mediterranean).

REMARKS
This genus resembles *Hemiaster* but differs in having an ethmolytic apical system. The genus remains poorly known.

Trachyaster oldhami (Noetling, 1897)

1897 *Hemiaster oldhami* Noetling, p. 36, pl. 8: figs 4-7
2000 *Trachyaster oldhami* (Noetlig); Smith & Jeffery, p. 344; text-fig. 141d-f

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3. THE PHYLOGENY OF THE CRETACEOUS SPATANGOIDS

3.1 INTRODUCTION

In this chapter I present phylogenetic analyses of the Cretaceous spatangoid families whose taxonomy has been revised in the previous chapter. I have included all species that are considered to be valid and are sufficiently well-known to be included in the analyses. I use cladistic parsimony analysis of morphological characters to produce hypotheses of evolutionary relationships. This technique attempts to reconstruct evolutionary history and groups taxa on the basis of derived characters that they share. For detailed accounts of phylogenetic methodology and terminology the reader is referred to Smith (1994), Kitching *et al.* (1998) or Felsenstein (2004).

3.2 PREVIOUS PHYLOGENETIC ANALYSES

As noted in the previous section, in recent years phylogenetic analyses have played an important role in shaping our understanding of the systematics of Cretaceous spatangoids. Important studies include:

- Smith (1984) provided a family level evolutionary tree of the echinoids including the spatangoids.
- Jeffery (1999) used phylogenetic methods to demonstrate that somaliasterids are likely to be spatangoids rather than holasteroids.
- Villier *et al.* (2004) carried out a detailed analysis of the early spatangoids in order to understand the radiation of the group.
- Stockley *et al.* (2005) presented morphological and molecular analyses of large datasets of fossil and living spatangoid genera.
- Barras (2007) carried out a thorough analysis of the 'disasteroid' echinoids showing how the spatangoids originated.

The general implications of these studies for spatangoid systematics are discussed in more detail in the previous chapter. Aspects of these studies

pertinent to the phylogeny of the various Cretaceous families are discussed below.

3.3 GENUS LEVEL ANALYSIS

In this chapter I begin by carrying out a phylogenetic analysis of the Cretaceous spatangoids at the genus level. I then subsequently carry out species level analyses of the major clades identified in the initial analysis.

3.3.1 TAXA AND OUTGROUP

All of the 37 genera of Cretaceous spatangoids that are sufficiently well known were incorporated into the analysis. Where the type species of the genus occurs in the Cretaceous I have used this to represent the genus; where it does not, a well-known Cretaceous representative was selected. Where characters were unknown in the type species, information from other species was used. *Toxaster retusus* was used as the outgroup for the analysis as it is one of the oldest species of spatangoid and is widely accepted to be one of the most basal (Villier *et al.* 2004; Stockley *et al.* 2005); this species was also used as the outgroup by Stockley *et al.* in their analysis of the spatangoids.

3.3.2 ANALYTICAL METHODS

The dataset was analysed using parsimony within the computer programme PAUP* (Swofford 2002). All characters were assigned equal weight and were treated as unordered. To construct the trees an initial heuristic search (1000 replicates; TBR; ACCTRAN) was carried out. Characters were then re-weighted according to their Rescaled Consistency Index (RCI) in the initial analysis. A second heuristic search (1000 replicates; TBR; ACCTRAN) was then carried out. A strict consensus tree was then used to summarise the information given in the Most Parsimonious Trees (MPTs).

The consistency index (CI) and retention index (RI) were both noted as measures of robustness. To produce an index of support, the bootstrap technique (Felsenstein 1985) was used (fast stepwise-addition, 1000 replicates). The results were presented on the strict consensus tree.

3.3.3 CHARACTER CODING AND DEFINITIONS

The taxa were coded for 45 morphological characters, which are a combination of characters gleaned from previous phylogenetic analyses of spatangoids (especially Jeffery 1998; Villier *et al.* 2004; Stockley *et al.* 2005) and novel characters (see data matrix in Table 3.3.1). These characters are listed and defined here:

Apical system

1. Position of apical disc: central (35-55% of test length from the anterior margin) (0); anterior (<35%) (1); posterior (>55%) (2). Most taxa have an approximately centrally positioned apical system, but in some, such as *Proraster*, it is posterior of centre, while in others such as *Coraster* it is anteriorly positioned.

2. Number of genital pores: four (0); three, genital plate two without opening (1); three, genital plate four without opening (2); two, genital plates two and three without openings (3). The majority of Cretaceous genera have a genital pore in each of the four genital plates. However, *Abatus pseudoviviparus* lacks pores in genital plates 2 and 3, *Orthaster* lacks a pore in genital plate 3, and *Isaster* and *Cyclaster* both lack a pore in genital plate 2.

3. Apical disc plating: ethmophract with ocular IV insert (0); ethmophract (1); semi-ethmolytic (2); ethmolytic (3). Apical disc plating is one of the most important characters in traditional spatangoid taxonomy; the most common

plating patterns are shown in Figure 3.3.1. In some spatangoids the posterior pairs of genital and ocular plates are both in contact with one another: this condition is termed ethmopract. Ethmophract species can be divided into those where ocular plate IV separates genital plates 3 and 4 (ocular plate IV insert), and those where it does not (ocular plate IV exsert). In the semi-ethmolytic condition, the posterior genital plates (but not the posterior ocular plates) are separated from one another by the madreporite (genital plate 2). If both the posterior ocular and genital plates are separated by the madreporite then the apical disc is termed ethmolytic. While this character has been considered to be very important in high-level spantangoid taxonomy, it is in fact very variable, even within individual species.

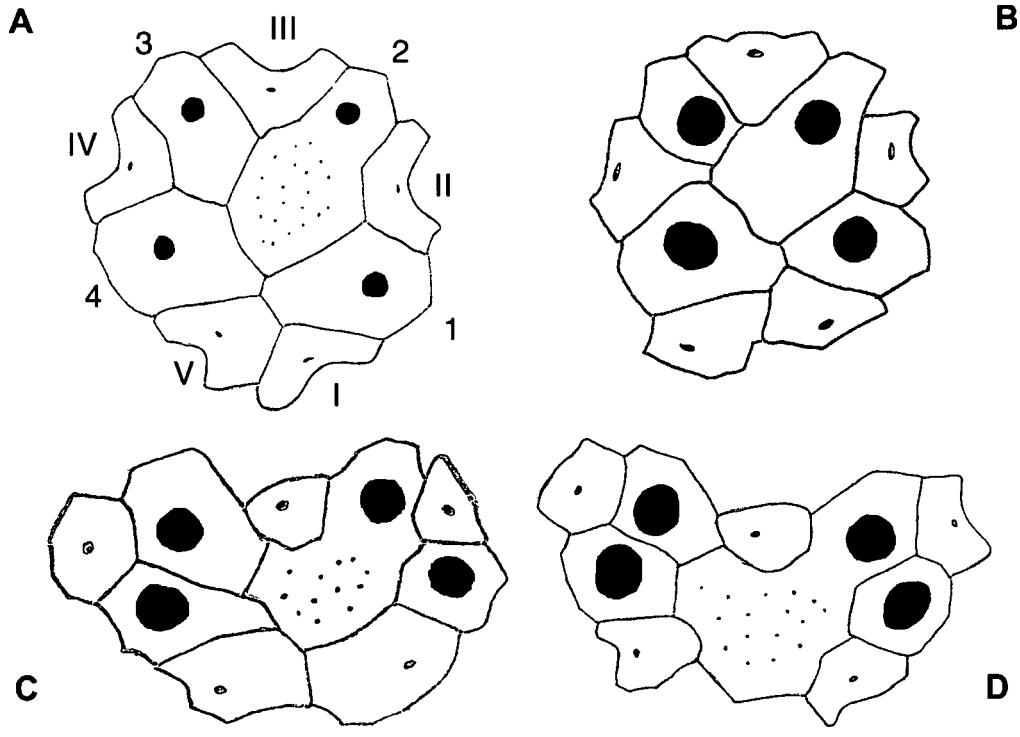

Figure 3.3.1: Apical systems of spatangoids. (**A**) Ethmophract with ocular plate IV exsert, genital plates numbered 1-4 and ocular plates numbered I-V; (**B**) ethmophract with ocular plate IV insert; (**C**) semi-ethmolytic; (**D**) ethmolytic.

Anterior ambulacrum

4. Depth of anterior ambulacrum midway between apex and ambitus: flush (0); shallowly concave (1); at least as deep as wide (2).

5. Depth of anterior ambulacrum at ambitus: flat or convex in plan view (0); shallowly concave in plan view (1); at least as deep as wide forming prominent notch in plan view (2).

6. Depth of anterior ambulacrum on oral surface: flush (0); shallowly concave without distinct edges (1); forming a distinct channel with sharply defined edges (2).

7. Length of petaloid part of anterior ambulacrum: extending 60-90% of the distance from the apical system to the ambitus (1); short, extending approximately 50% of the distance from the apical system to the ambitus (0).

8. Pores in anterior ambulacrum: uniform (0); heterogenous (1). Most taxa have pores of uniform width in the anterior ambulacrum, but *Heteraster* has some narrow pore-pairs and some wide pore-pairs.

9. Type of pore pairs in anterior ambulacrum: oval pore-pairs (0); asymmetrical, elongate pore-pairs (1). The type of pore-pair in the anterior ambulacrum can be used to infer the nature and function of the tube feet in life (see Smith 1980).

10. Width to length ratio of plates in anterior ambulacrum (measured midway between the apical system and ambitus): <1.5 (0); 1.5-5.0 (1); >5.0 (2).

Paired ambulacra

11. Relative lengths of anterior and posterior petals (equipetality): 1.0-1.5 (0); >1.5 (1); <1.0 (2). Spatangoids vary from having paired petals that are

equal in length (e.g. *Mecaster*) to having the anterior pair more than three times the length of the posterior pair (e.g. *Leymeriaster*). Apetaloid taxa are scored '?' for this character.

12. Paired petals: flush (0); sunken (1). Where petals are extremely deeply sunken to form marsupia (brood pouches) this is not coded as a distinct character in order to ensure that the phylogeny remains independent of data relating to larval strategy.

13. Divergence of anterior paired petals at longest straight part: 90-130° (0); >130° (1); <90° (2). Most genera have anterior paired petals that diverge at approximately 100°, but some taxa e.g. *Mauritanaster* have very divergent paired petals, while others, e.g. *Proraster* have petals that run close to parallel to the anterior groove.

14. Axis of paired petals: straight (0); anterior and/or posterior paired petals sinuous (1); weakly curved near apex (2).

15. Type of pore-pairs in paired ambulacra: oval pore-pairs (0); asymmetrical elongate pore-pairs (1); slit-like, symmetrical elongate pore-pairs (2).

16. Pore-pairs strongly reduced in anterior branch of anterior ambulacrum: no (0); yes (1).

17. Distal termination of petals: petal pore-pairs decrease in size gradually and there is no abrupt end to the petals (0); petals end with an abrupt decrease in pore size (1).

18. Termination of paired posterior petals: sub-petaloid (0); divergent (1); closed (2). In petaloid taxa the petals may end by the two branches coming

closer together (closed e.g. *Hemiaster*), or further apart (divergent e.g. *Toxaster*).

19. Ambulacra pinched at ends of petals: no (0); yes (1). In *Holanthus* and *Proraster* the ambulacra are strongly pinched just below the terminations of the petals.

20. Petal shape: the two columns parallel along their length (0); petals lanceolate: widened in the middle and converging distally (1); petals gradually widening distally (2).

21. Anterior paired petal length: short, extending only about half the distance to the ambitus (0); extending between 0.6 and 0.9 of the radial length (1); reaching the ambitus in plan view (2). Apetaloid taxa are coded '?'.

22. Pore-pairs in petals: the two columns closely spaced leaving almost no perradial zone (0); separated by more than 1.5 times the pore-pair width (1).

23. Very broad and strongly bowed petals: no (0); yes (1). *Holanthus* and *Leiostomaster* have very broad and strongly bowed petals in comparison to other Cretaceous spatangoids.

Interambulacra and plastron

24. The number of the ambulacral plate abutting the rear suture of the labral plate in interambulacrum I: one (0); two (1); three (2); four or more (3).

25. The number of the ambulacral plate abutting the rear suture of the sternal plate in interambulacrum I: five (0); six (1); seven or eight (2); nine or more (3); three or four (4).

26. Suture between labral and sternal plates: straight (0); strongly curved (1).

27. Suture between sternal plates: oblique with plate 2a extending considerably further towards ambitus than 2b (0); oblique with suture between 2a and 3a approximately level with that between 2b and 3b; vertical – sternal plates symmetrical (2). This character is illustrated in Figure 3.3.2.

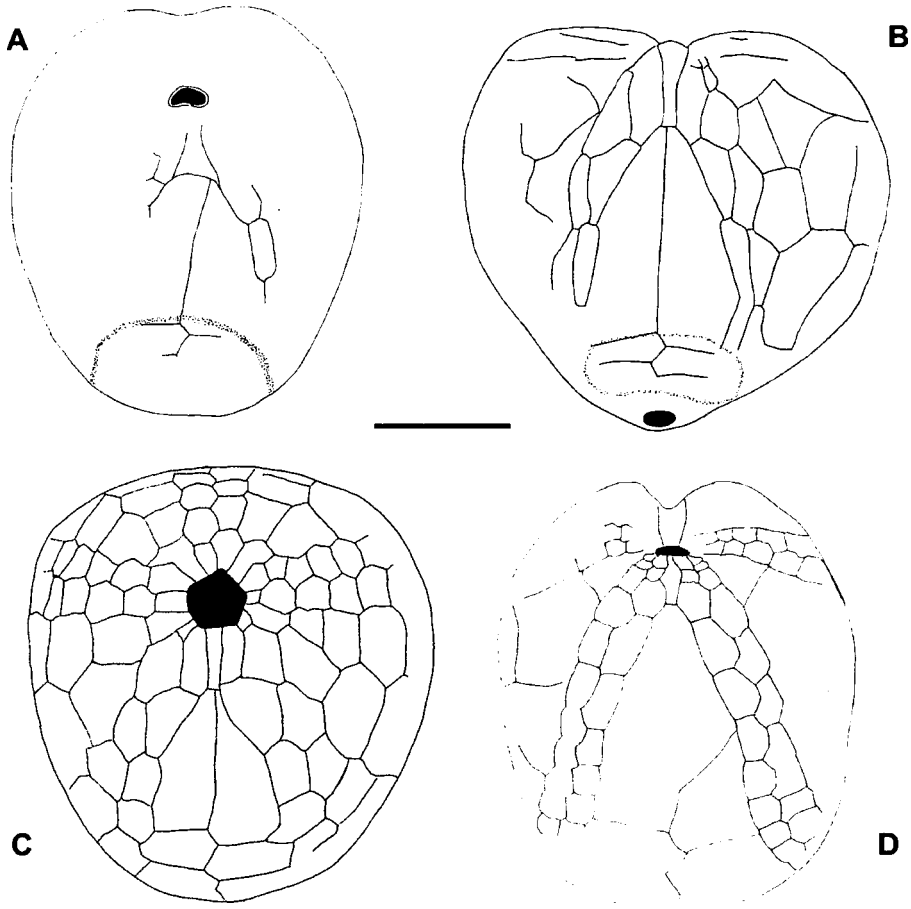

Figure 3.3.2: Lower surface characters. (**A**) *Diplodetus americanus* (USNM 76285) showing a peristome that faces obliquely forwards and an oblique sternal suture; (**B**) *Micraster coranguinum* (BMNH E32820) showing the peristome completely hidden by the labral plate and symmetricalsternal plates; (**C**) *Homoeaster inflatus* (MNHN J01094) showing a pentagonal downward facing peristome and meridoplacous plating on the left and amphiplacous plating on the right when viewed from below; (**D**) *Iraniaster bowersi* (USNM 170506) showing a peristome that faces obliquely forward and a labral plate in contact with only one sternal plate. Relative scale bar: A: 9.6 mm; B: 17.6mm; C: 9.0 mm; D: 20.5 mm.

28. Labral plate: in contact with both sternal plates (0); in contact with only sternal plate 2b (1).

29. Interambulacra 1 and 5: both amphiplacous (0); one meridoplacous, one amphiplacous (1); both meridoplacous (2). In the amphiplacous condition the first ambulacral plate from the mouth is in contact with two plates; in meridoplacous taxa this plate is in contact with a single plate.

30. Plastron: widening to the rear (0): more or less parallel sided (1).

31. Length of labral plate relative to that of sternal plates: <20% (0); 20-50% (1); >50% (2).

Peristome

32. Position of peristome: >15% of test length from the anterior margin (0); <15% of test length from the anterior margin (1).

33. Peristome shape: circular to ovate, e.g. *Hemiaster* (0); distinctly pentagonal, e.g. *Homoeaster* (1).

34. Peristome orientation: downward-facing (appears ovate or pentagonal when viewed from below, labrum not projecting below plane of opening) (0); obliquely facing forwards (labral plate strongly projecting so peristome appears kidney-shaped) (1); vertical (peristome almost entirely hidden by labral plate in plan view) (2).

35. Peristome surrounded by a distinct rim: no (0); yes (1).

Periproct

36. Shape of periproct: round or wider than high (0); high with pointed tips (1).

Fascioles

Fasciole characters are illustrated in Figure 3.3.3.

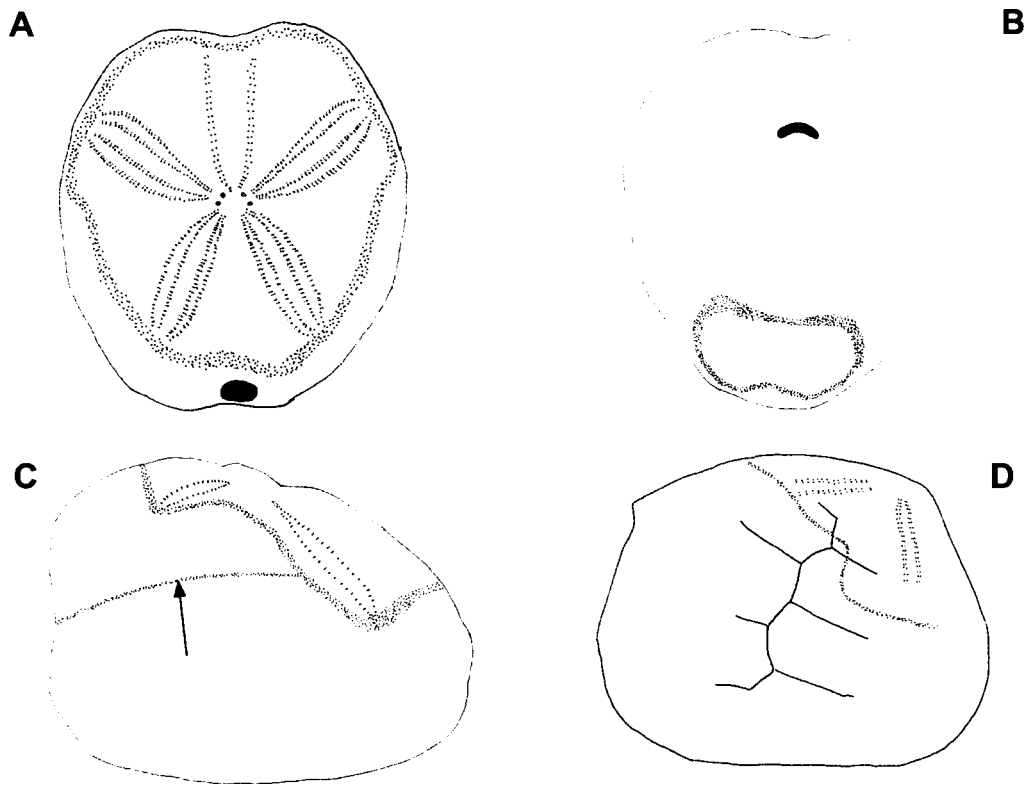

Figure 3.3.3: Spatangoid fascioles. (**A**) Peripetalous fasciole; (**B**) sub-anal fasciole; (**C**) latero-anal fasciole (arrow); (**D**) peripetalous fasciole passing some distance from the petal ends.

37. Peripetalous fasciole: absent (0); present (1). Some spatangoids have a fasciole (band of very small tubercles) that runs around the ends of the petals; this is termed a peripetalous fasciole.

38. Peripetalous fasciole: independent of other fascioles (0); unites with marginal fasciole around anterior (1). In schizasterids, a marginal fasciole

typically diverges from the peripetalous fasciole behind the anterior paired petals, it then runs around the margin of the test and beneath the anus.

39. Peripetalous band in lateral interambulacra: not indented (0); indented behind anterior paired petals (1). In some taxa the peripetalous fasciole is strongly indented behind the anterior paired petals (e.g. *Schizaster*), whereas in others it is not (e.g. *Iraniaster*).

40. Fasciole bounds the ends of the anterior paired petals: yes (0); no (1). The peripetalous fasciole usually runs immediately below the termination of the anterior paired petals. However, in some taxa (e.g. *Holcopneustes*) it runs some distance below the ends of the petals.

41. Subanal fasciole ring: absent (0); present (1). Micrasterids typically have a closed fasciole ring below the anus.

42. Fasciole crossing posterior interambulacrum below anus and continuing as a marginal/lateroanal band: absent (0); present (1).

43. Aboral tuberculation with small primary tubercles set in a groundmass of fine dense uniform granules: no (0); yes (1). Micrasterids tend to have this characteristic tuberculation (Smith & Jeffery 2000).

Test shape

44. Posterior end of the test: rounded (0); truncated (1); prominent heel (2).

45. Test with prominent nodules on the lower surface: no (0); yes (1). *Tessieria* has series of prominent nodules adjacent to the plastron.

Toxaster	0001110011	?121100102	1103110000	2000000000	00010
Heteraster	0001110112	0021110102	1?03200000	2000000000	00010
Mokotibaster	0020010?12	0000?00100	200320207?1	2000000- - 0	00000
Macraster	0011110011	0102100100	2003210000	1011001000	00010
Epiaster	0021110011	0000200101	1102110?0	?000110- - 0	00100
Pliotoxaster	0021110012	0102200101	100??100?0	?000000000	000?0
Iraniaster	0021110001	0102201100	10021- 0110	1100001000	00010
Palhemiaster	0021110000	0102101201	1002?100?0	1010011010	00010
Mecaster	00(23)1110002	0102201201	1002202?0	1011011010	00010
Lambertiaster	0031110000	0100201200	1003102000	2010?01011	00010
Holcopneustes	1031110002	0100201200	100??020?0	?0?1??1001	00010
Polydesmaster	0022211002	0100(12)01200	1101200000	0001001 0?0	01010
Periaster	00(12)1110001	0102101201	1001102001	0001011110	01010
Abatus	2331100001	0122101201	1100102000	0001011110	01010
Linthia	0031110001	0102101201	1001002001	0011011110	01010
Schizaster	003111?001	1102101201	1001002000	0001011110	01010
Tessieria	0031110001	1102101201	100??020?0	0001011110	01011
Holanthus	0011000001	0100101211	1011(01)02000	1000001010	00010
Leiostomaster	0021001000	0102?01201	101??120?0	?0101010?0	00010
Bolbaster	0011000001	1100001201	10010020?0	1001001000	00000
Hemiaster	0011110001	1100001201	1002110000	1001101000	00010
Leymeriaster	0021001002	1100101201	100??110?0	?001111010	00010
Proraster	2022211001	1121111211	1001002000	1001011000	00010
Mauritanaster	103111?000	2110101201	200??020?1	?0010?10?0	??010
Heterolampas	0021010011	2110101201	2003302000	1000011000	00010
Plesiaster	00111?0001	0102101101	1101010000	1011000- - -	10110
Diplodetus	0011110002	0100?01100	0?01002000	1002100- - -	10110
Gibbaster	0011211012	0102?00100	1001102011	11?2000- - -	10110
Isaster	011000100?	0100?00100	0001(01)02000	2000100- - -	10100
Cyclaster	0111111001	0100(12)01100	0001102001	1102001010	10110
Micraster	00(12)1110001	0102100000	1001002001	1102000- - -	10110
Turanglaster	0010?1?00?	?00?000002	??03001000	2111000- - -	10110
Ovulaster	101111?00?	?110(03)00002	?102002001	20?1000- - -	10110
Homoeaster	1011110001	0112100002	2001002000	2011001001	00010
Orthaster	121011?002	?010000002	?101?020?1	2101001010	00010
Coraster	102001?001	?010(03)00002	?101402021	200200101-	00010
Cottreaucorys	101001?001	?010000002	??01402001	200100101-	00020

Table 3.3.1: Data matrix used in the genus level phylogenetic analysis.

3.3.4 RESULTS AND DISCUSSION

The initial heuristic search produced 683 MPTs of 223 steps with CI 0.314 (0.305 with uninformative characters excluded) and RI 0.557. When the analysis was repeated after *a posteriori* character re-weighting according to RCI three MPTs were recovered with CI 0.426 (0.392 with uninformative characters excluded) and RI 0.652. The three MPTs differed only in the postion of *Epiaster*. A strict consensus tree was used to summarize the

relationships common to all three MPTs; this is presented in Figure 3.3.4 with bootstrap values (≥ 50%) displayed above each branch. While statistical support for many of the clades recovered is low, the support values are comparable to those found in other genus level analyses of fossil irregular echinoids (e.g. Smith 2004; Barras 2006, 2007).

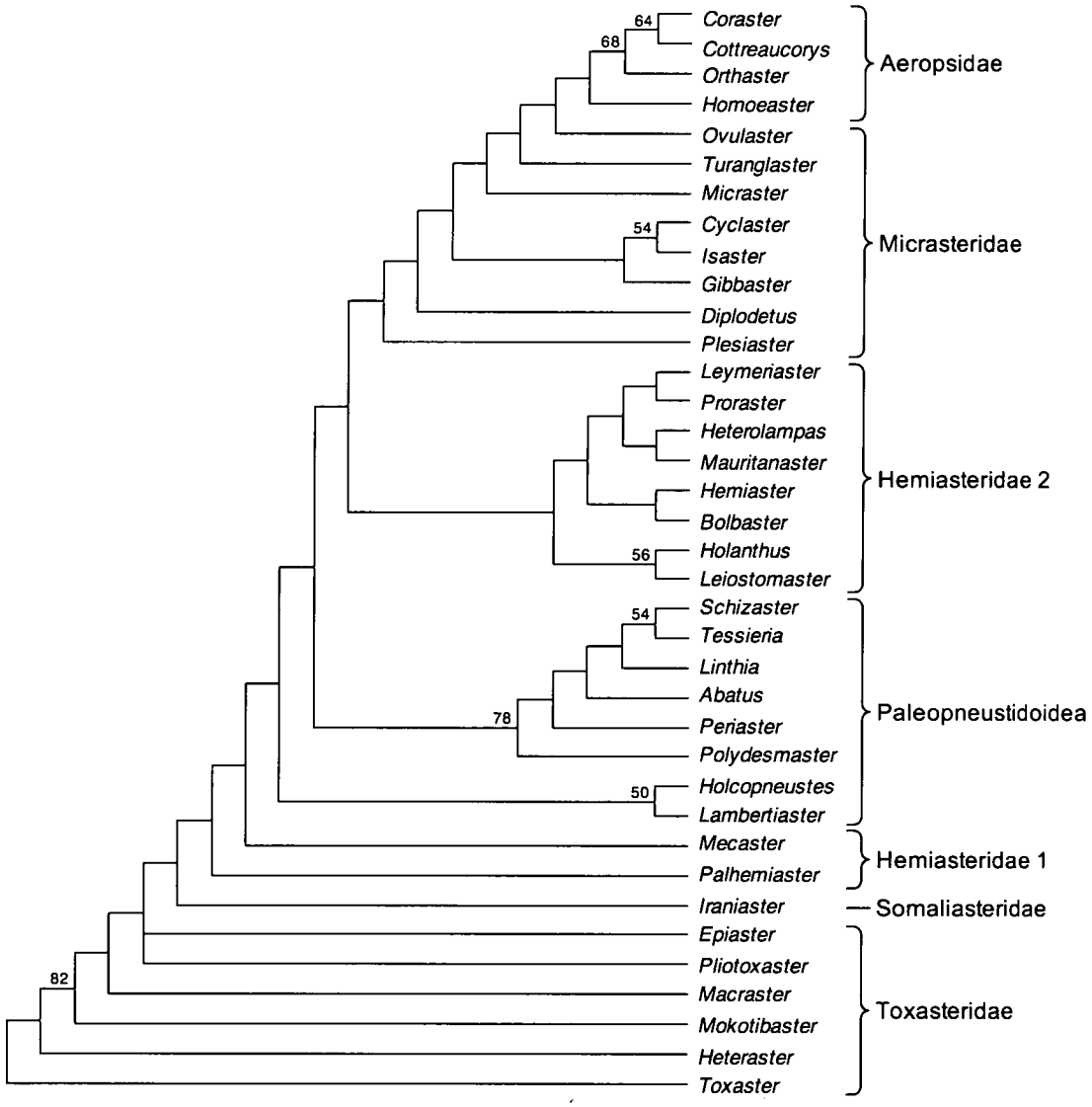

Figure 3.3.4: Strict consensus tree of Cretaceous spatangoid genera. See text for details of phylogenetic analysis. Bootstrap values, where above 50%, are displayed above branches.

Most of the major groups of spatangoid are recovered though many of them do not form monophyletic groups. The toxasterids form a basal paraphyletic grade as they do in the analyses of Villier *et al.* (2004) and Stockley *et al.* (2005).

The hemiasterids form a polyphyletic group in this analysis with *Mecaster* and *Palhemiaster* making up a paraphyletic grade basal to the paleopneustine taxa and the remaining genera forming a distinct monophyletic group. Unlike the findings of Villier *et al.* (2004) the analysis did not recover a monophyletic Hemiasterina (hemiasterids plus schizasterids) clade, but rather recovered it as a paraphyletic group as found by Stockley *et al.* (2005).

The paleopneustids form a paraphyletic group (unlike in the analysis of Stockley *et al.* (2005) where it was monophyletic), although each of the constituent groups, the schizasterids and the prenasterids, form monophyletic clades. *Polydesmaster* is found to lie in the stem group of Schizasteridae, rather than that of Paleopneustoidea as found by Stockley *et al.* (2005).

The aeropsids and micrasterids form a monophyletic clade in this analysis. The origins of the aeropsids is poorly known, but the group has generally been thought to be derived from the hemiasterine spatangoids (e.g. Fischer 1966; Smith 2005). Villier *et al.* (2004) did not include any aeropsid species in their phylogenetic analysis. Stockley *et al.* (2005) did include several and found them to form the most basal clade in the analysis (aside from the outgroup *Toxaster*). The position of the aeropsids in the present analysis seems to result from the inclusion of the micrasterid genera *Ovulaster* and *Turanglaster*, which are similar in morphology to the aeropsids. It remains to be seen whether this is an artefact caused by convergence or a genuine phylogenetic relationship revealed by increased sampling resolution. As

there are extant representatives of hemiasterids, micrasterids and aeropsids, the origin of the aeropsids could be studied in an independent way by incorporating molecular data on these groups into the molecular phylogenies of Stockley *et al.* (2005).

I have elected to retain names such as Hemiasteridae and Micrasteridae in the taxonomic revision presented in the previous chapter, even though this analysis does not find them to be monophyletic clades. I consider it premature to overhaul the higher-level taxonomy of the group based on a single analysis without very strong statistical support. Future molecular work is likely to provide new data to refine the phylogenetic hypotheses proposed here.

3.4 AEROPSIDAE

3.4.1 TAXA AND OUTGROUP

I have, to my knowledge, included all species of aeropsid whose morpholology is sufficiently well known to be included in the data matrix. The few post-Cretaceous species of aeropsid are included for completeness. *Hemiaster bufo* was used as the outgroup for the analysis because, although the precise position of the aeropsid clade within the spatangoids is subject to some uncertainty, it is generally thought to lie within Hemiasterina (e.g. Fischer 1966; Smith 2005; but see also results of genus level analysis above).

3.4.2 ANALYTICAL METHODS

All analyses were carried out using the computer programme PAUP (Swofford, 2002). All characters were assigned equal weight and were treated as unordered. Unknown and inapplicable entries were both entered as '?' and treated as missing data.

The dataset was too large for an exhaustive search, but small enough that a branch and bound search could be used to find the most parsimonious trees (MPTs). The simple addition sequence offered within PAUP was used. A strict consensus tree was used to summarize the information given in the MPTs.

The consistency index (CI) and retention index (RI) were both noted as measures of robustness. The bootstrap technique (Felsenstein 1985) was used to produce an index of support. A full heuristic search was carried out using 1000 replicates. The results were presented on the strict consensus tree. A decay analysis (Bremer support) (Bremer 1988, 1994) was carried out using the computer programme TREEROT (Sorensen 1999) in order to provide a measure of relative support for each clade. The decay index of a particular clade represents the number of additional steps required for a clade to be removed from the tree. The decay indices were also presented on the strict consensus tree.

3.4.3 CHARACTER CODING AND DEFINITIONS

Each species was coded for 24 morphological characters (see data matrix in Table 3.4.1). These characters are listed and discussed below.

Apical System

1. Number of gonopores in the apical system: four (0); three (1); two (2). Most aeropsids have four gonopores in the apical system, but some (e.g. *Aeropsis rostrata*) have two; *Orthaster* has three.

2. Plating of the apical system: ethmophract with ocular plate IV exsert (0); ethmophract with ocular plate IV insert (1); semi-ethmolytic (2). In taxa with reduced or fused plating this character is scored as a '?'.

3. Number of genital plates in the apical system: four (0); two (1); one (2). In most taxa the apical system has four genital plates. However, in *Aeropsis rostrata*, *Sphenaster larumbensis* and *Cottreaucorys kollmani* plates are reduced or fused so that there are only two genital plates (one on each side). Smith (2005) illustrated the holotype of *Aeropsis fulva*, which appears to have all four genital plates fused.

4. Position of the apical system: 30-50% of test length from the anterior margin (e.g. *Sphenaster*) (0); less than 30% of test length from the anterior margin (e.g. *Aeropsis*) (1).

Anterior ambulacrum

5. Anterior ambulacrum: with small pore pairs (0); with enlarged pore pairs (1). *Aeropsis* and *Sphenaster* have enlarged pore pairs associated with funnel-building tube feet, whereas the taxa previously assigned to the corasterids have small, undifferentiated pore pairs.

6. Anterior ambulacrum: flush near to the apex (0); depressed near to the apex (1). In *Sphenaster* and *Aeropsis* the part of the anterior ambulacrum closest to the apical system is depressed.

7. Anterior ambulacrum: flush to weakly depressed at the ambitus (0); deeply sunken at the ambitus (1). *Cottreaucorys sulcatus* differs from the other aeropsid genera in having a deeply sunken frontal groove.

8. Depth of the anterior ambulacrum on the lower surface: sunken (0); flush (1). In *Aeropsis* and *Sphenaster* the anterior ambulacrum is flush on the lower surface, but in the corasterids it is generally sunken.

Paired ambulacra

9. Paired ambulacra: apetaloid or sub-petaloid (0); petaloid (1). Most aeropsids are apetaloid to sub-petaloid, but *Cottreaucorys sulcatus* has moderately well developed petals.

10. Paired ambulacral plating on aboral surface: plates low and wide (> twice as high as wide) (0); plates high (<1.5 times wider than high) (1). In most aeropsid taxa the plates of the paired ambulacra are relatively high, but *Homoeaster* has low wide plates.

Plastron and interambulacra

11. Lateral paired interambulacra: both meridoplacous (0); one meridoplacous and one amphiplacous (1); both amphiplacous (2).

12. Relative lengths of labral and sternal plates: labral plate less than two thirds as long as the sternal plates (0); labral plate at least two thirds as long as the sternal plates (1).

13. Length to width ratio of sternal plates: approximately twice as long as wide (0); at least 2.5 times as long as wide (1).

Peristome and periproct

14. Shape of peristome: circular or ovate (0); pentagonal (1). Most taxa have a peristome with a rounded outline, but *Homoeaster* has an angular, pentagonal peristome.

15. Postion of peristome: more than 10% of test length from the anterior margin (0); less than 10% of test length from the anterior margin (1).

16. Orientation of peristome: obliquely forwards (0); downwards (1).

17. Size of the peristome: small (<15% maximum test width) (0); large (>15% maximum test width) (1).

18. Periproct: not clearly visible from above (0); clearly visible from above (1). In some taxa (e.g. *Aeropsis*) the periproct is supra-ambital and clearly visible in apical view.

19. Size of the periproct: small (<15% maximum test width) (0); large (>15% maximum test width) (1).

Fascioles

20. Position of the peripetalous fasciole: runs closer to the ambitus than to the high point of the test in the posterior interambulacrum (e.g. *Homoeaster*) (0); passes close to the high point of the test in the posterior interambulacrum (e.g. *Coraster*) (1).

21. Peripetalous fasciole: sharply kinked behind anterior paired petals (e.g. *Homoeaster tunetanus*) (0); undulose path (e.g. *Homoeaster evaristei*) (1).

Test shape

22. Test shape in profile: sub-globular (e.g. *Coraster*) (0); sub-conical (e.g. *Homoeaster*) (1); wedge-shaped to cylindrical (e.g. *Sphenaster*, *Aeropsis*) (2).

23. Subanal heel: absent or weak (0); strongly pronounced (1). The genera *Aeropsis*, *Spenaster* and *Cottreaucorys* have a posterior face that projects to form a pronounced heel beneath the periproct.

24. Test shape: test less than twice as long as wide (0); greater than twice as long as wide (1). *Aeropsis* has an extremely elongate form, which makes it instantly recognizable.

OUTGROUP	00000	01010	00000	00000	0000
Sphenaster larumbensis	2?101	10111	?1000	01111	0210
Aeropsis rostratus	0?111	10111	00000	11111	0211
Aeropsis fulva	2?211	10111	00000	11111	0211
Cordastrum sulcatus	00010	01001	00000	00101	?010
Homoeaster evaristei	00000	00010	?0110	00000	0100
Homoeaster tunetanus	01000	00010	?0110	00000	1100
Homoeaster auberti	01000	00010	00110	00000	?100
Cottreaucorys blayaci	01010	00011	00000	00111	1010
Cottreaucorys kollmani	2?110	00011	?1000	0111?	?010
Coraster vilanovae	01010	00011	1000A	00001	1000
Coraster beneharnicus	02010	00011	?0000	00001	1000
Orthaster alievi	11000	00011	?0000	00001	?000
Orthaster dagestanensis	11000	00011	?0001	00001	1000

Table 3.4.1: Data matrix used in the phylogenetic analysis of the aeropsids. 'A' represents character states 0 and 1.

3.4.4 RESULTS AND DISCUSSION

The branch and bound search produced six MPTs of 37 steps with CI 0.757 (0.735 with uninformative characters removed) and RI 0.847. A strict consensus tree was used to summarize the relationships common to all six MPTs; this is presented in figure 3.4.1 with bootstrap and decay indices displayed above and below each branch respectively.

The analysis recovers a well-supported clade containing *Aeropsis* and *Sphenaster* (bootstrap support value = 92; decay index = 4) supporting the suggestion of Smith (2005) that *Sphenaster* is the sister taxon of *Aeropsis*. Basal to this group lies a paraphyletic grouping of species previously assigned to the genera *Cottreaucorys* and *Cordastrum*. The clade of *Aeropsis + Sphenaster + Cottreaucorys* also represents a moderately well-supported grouping (bootstrap support value = 58; decay index = 2). These

relationships support the notions outlined by Kroh (2004) that *Cottreaucorys* represents a link between *Aeropsis* plus *Sphenaster* and the corasterids, and that the former group evolved from the latter by the gain of a pronounced keel and specialization of the tube feet in the anterior ambulacrum. In fact, *Cottreaucorys* itself has been variously assigned to either the corasterids (e.g. Smith & Jeffery 2000, Smith 2005) or the aeropsids (e.g. Kroh 2004). Basal of the *Aeropsis + Sphenaster + Cottreaucorys* clade is a paraphyletic group containing the 2 species of *Coraster*, with the *Aeropsis + Sphenaster + Cottreaucorys + Coraster* clade being weakly supported (bootstrap support value = 45; Decay index = 1). *Aeropsis + Sphenaster + Cottreaucorys + Coraster + Orthaster*, however, represents a fairly strongly supported clade (bootstrap support value = 78; decay index = 2) with *Homoeaster* representing the most basal aeropsid. These findings are contrary to the suggestion of Smith & Jeffery (2000) that *Cottreaucorys* should be placed under the synonymy of *Homoeaster*. However, a closer relationship between *Cottreaucorys* and *Coraster* is supported by a series of specimens from Alicante, Spain that seem to represent morphological intermediates between *Coraster* and *Cottreaucorys* in which the subanal heel is variably developed (See Section 2.3).

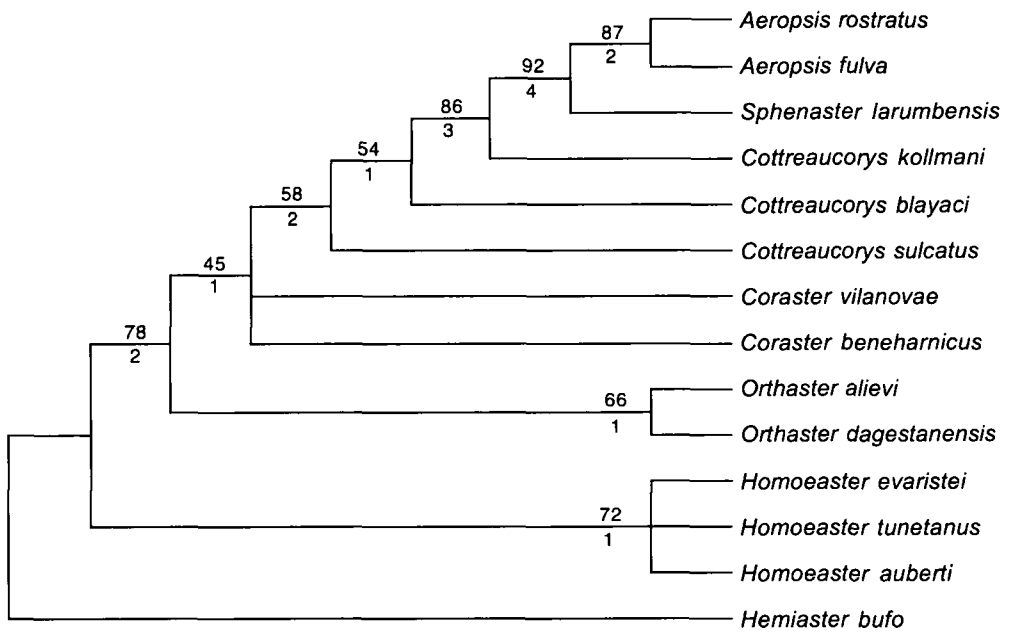

Figure 3.4.1: Strict consensus of the six MPTs for the Aeropsidae. Bootstrap support values are given above the branch leading to each node; decay indices are given below the branch.

3.5 HEMIASTERIDAE

3.5.1 TAXA AND OUTGROUP

The hemiasterids form a polyphyletic group in the genus level analysis presented in Section 3.3. As a result, it is not appropriate to analyse them in isolation: their relationships need to be considered along with those of closely related taxa. Here I present an analysis that incorporates each of the hemiasterid species considered valid as well as each of the proposed species groups of *Hemiaster*, *Bolbaster* and *Mecaster* and a representative of each of the non-hemiasterid spatangoid families. These taxa are listed in the data matrix, which is presented in Table 3.5.1. *Toxaster* is used as the outgroup as it is the representative of the toxasterids, which are accepted to be a basal grade within the spatangoids.

3.5.2 ANALYTICAL METHODS

The analytical methods used in this analysis are identical to those used for the genus level analysis, with the exception that the results are displayed on a 50% majority rule tree, rather than a strict consensus tree.

3.5.3 CHARACTER CODING AND DEFINITIONS

The data matrix is presented in Table 3.5.1. The characters used in this analysis are the same as those used in the genus level analysis plus the following additional characters:

46. Apical system: narrow (e.g. *Mecaster batnensis*) (0); wide (*Mecaster fourneli*) (1).

47. Divergence of posterior paired petals: <120° (0); very divergent (>120°) (1).

48. Position of the highest point of the test: anterior of the apical system (0); at or immediately behind the apical system (1); well behind the apical system (2).

49. Posterior face: vertical or sloping outwards (0); overhanging (1).

50. Length of test: approximately equal to test width (0); longer than 1.1 times test width (1).

51. Ridges running between pore-pairs of the anterior ambulacrum and the edges of the ambulacrum: absent (0); present (e.g. *Leymeriaster maestrichtensis*).

52. Genital plates G2 and G4: in contact (0); separated by genital plate 3 and ocular plate V.

Toxaster	0001110011?121100102110311000020000000000000101010000
Iraniaster	00211100010102201100100 21-0110110000100000010101000 0
P. peroni	0021110000010210120120 02?100?0101001101000010101000 0
P. calvini	0021110000010210120110 02?100?0101001101000010101000 0
P. ibericus	0021110000010210120110 02?100?0101001101000010101000 0
M. batnensis	0021110002010220120110022010?0101101101000010101000 0
M. fourneli	0031110002010220120110022020?0101101101000010201000 1
M. scutiger	002111000201022012011 0220?0?0101101101000010101000 1
M. cubicus	0021110002010220120110022010?0111101101000010201000 0
M. africanus	0021110002010220120110022010?0101101101000010101000 0
M. aumalensis	0021110002010220120110122 0?0?0101101101000010101000 0
M. victoris	0031110002010220120010022010?0101101101000010101000 0
Lambertiaster	0311100000100201200100310200020 10?0101100010101000 0
Holcopneustes	1031110002010020120010 0??020?0?0?1??1001000101010000
Polydesmaster	00222110020100(12)012001101200000000010010?0010101010000
Periaster	00(12)11100010102101201100110200100010111100101010100 00
Abatus	2331100001012210120111001020000001011110010101010000
Linthia	0031110001010210120110010020010011011110010101020000
Schizaster	003111?0011102101201100100200000010111100101010100 00
Tessieria	0031110001110210120110 0??020?0000101111001011101000 0
H. hawkinsi	00110000010100101211101 1(01)020001000001010000101020000
Leiostomaster_sp	0021001000010 2?01201101??120?0?0101010?0000101010000
B. prunella	0011000001110000120010010020?0100100100000000101000 0
B. punctatus	0011000001110000120110010020?0100100100000000101000 0
Hemiaster	0011110001110000120110021100001001101000000101020000
L. sexangulatus	0021001002110010120110 0??110?0?0011110100001010100 00
L. madagacariensis	0021001002110110120110 0??110?0?0011110100001010100 00
L. micranthus	2021001002110010120110 0??110?0?0011110100001010200 00
L. eluvialis	0021001002110010120110 0??110?0?0011110100001010000 10
L. maestrichtensis	0021001002110010120110 0??110?0?0011110100001010100 10
L. regulusi	0021001002110010120110 0??110?0?0011110100001010100 10
L. nucleus	0021001002110010120110 0??110?0?0011110100001010100 00
L. similis	0021001002110010120110 0??110?0?0011110100001010100 00
L. leymeriei	0021001002110010120110 0??110?0?0011110100001010100 00
P. atavus	1002211001210111121110010020001001011000000101000000
P. geayi	2012211001212111121110010020001001011000000101110000
P. granti	2012211001212111121110010020001001011000000101110000
P. herrerae	1022211001110111121110010020001001011000000101000000
P. morgani	(12)012211001212111121110010020001001011000000101110000
M. mirabilis	103111?0002110101201200 ??020?1?0010?10?0??0101020000
H. maresi	0021010011211010120120033020001000011000000101020000
Micraster	00(12)11100010102100000100100200111020 00---101101011000
Homoeaster	1011110001011210000220010020002011001001000101010000

Table 3.5.1: Data matrix used in the phylogenetic analysis of the hemiasterids.

3.5.4 RESULTS AND DISCUSSION

The initial heuristic search produced 1741 MPTs of 133 steps (CI = 0.191; RI = 0.442). When the analysis was repeated with characters reweighted

according to Rescaled Consistency Index 6 MPTs of 48.94 steps were recovered (CI = 0.191; RI = 0.415). The 50% majority rule consensus of these trees is presented in Figure 3.5.1, with bootstrap support values displayed above the branches leading to each node.

All the hemiasterid genera form monophyletic clades and the higher-level relationships are broadly similar to those produced in the genus level analysis. One important difference is that *Holcopneustes* (the representative of the prenasterids) is sister group to the micrasterids plus the aeropsids, rather than lying basal to the schizasterids. In addition, *Hemiaster* lies at the base of the hemiasterid clade, rather than lying in a derived position. While the present analysis is thought to be a reasonable estimate of the phylogenetic relationships within the hemiasterid genera, I consider the genus level analysis to be a better estimate of the higher-level phylogeny, as a larger number of genera are sampled.

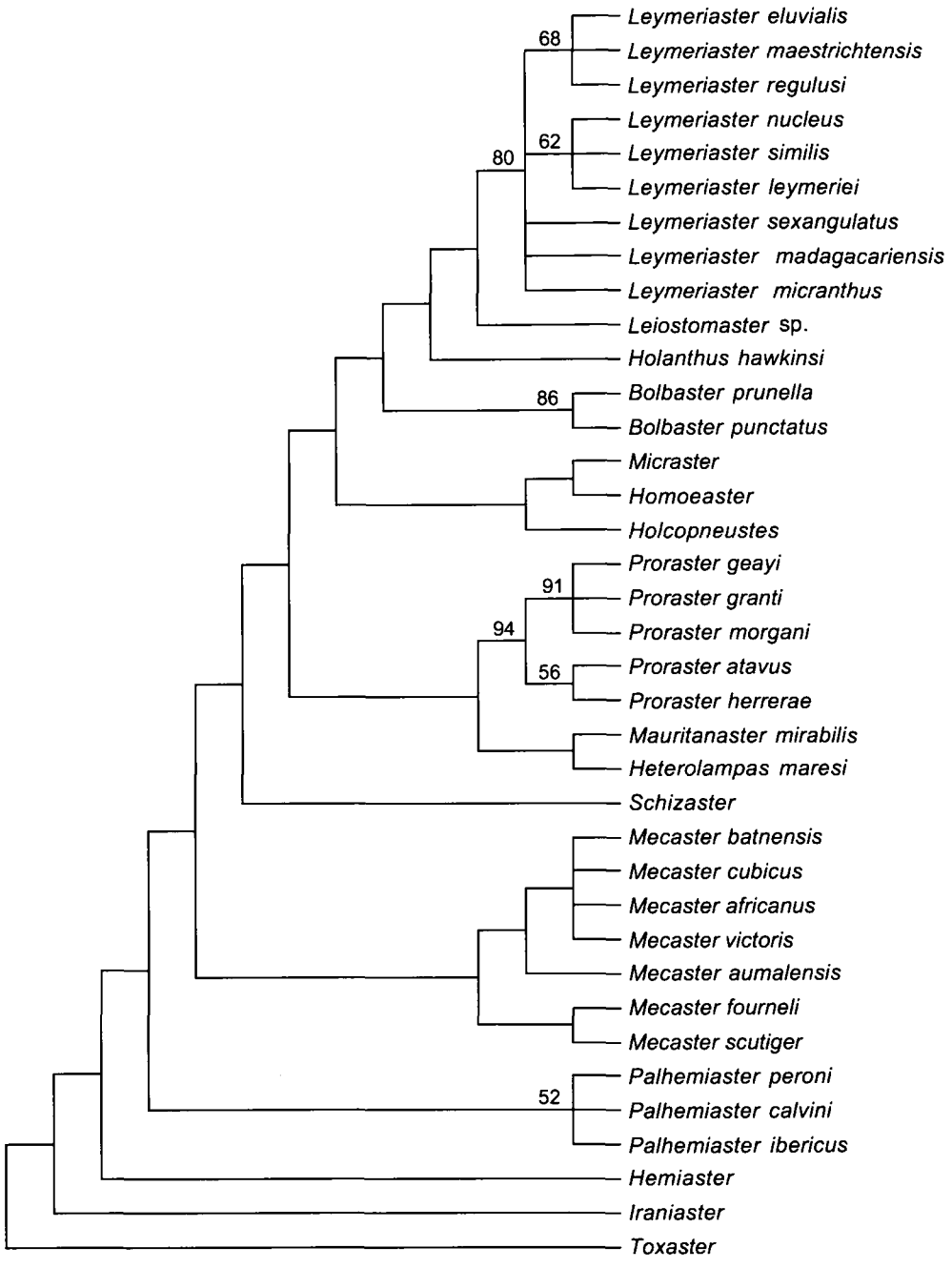

Figure 3.5.1: Strict consensus tree produced by the phylogenetic analysis; see text for analytical methods. Bootstrap support values, where over 50, are displayed above the branches leading to each node.

3.6 MICRASTERIDAE

3.6.1 TAXA AND OUTGROUP

I include all micrasterid species that I consider to be valid and for which sufficient data exists. The exceptions to this are the genera *Micraster* and *Gibbaster*. Over one hundred species of *Micraster* have been described from the Cretaceous alone (see taxonomic revision in section 2.5). These species are differentiated largely on subtleties of test shape and postition of the peristome. Here I include only the type species *M. coranguinum*. *Gibbaster* is also made up of many nominal species; here I include an example with a subanal fasciole (*G. gibbus*) and one without (*G. senonensis*).

The toxasterid genus *Epiaster* is widely thought to be paraphyletic with respect to the micrasterids (e.g. Smith 2005). I thus chose a representitive species, *E. breyniusi* as the outgroup for this analysis.

3.6.2 ANALYTICAL METHODS

The methodology used for this analysis is identical to that used in the phylogenetic analysis of the aeropsid spatangoids presented in section 3.4, with the following exceptions: (1) a heuristic search (rather than branch and bound) was used due to the larger size of the dataset; and (2) both strict and 50% majority rule consensus trees are presented.

3.6.3 CHARACTER CODING AND DEFINITIONS

The taxa were scored for 29 morphological characters. Characters are a mixture of new characters and those gleaned from the literature. In particular, Jeffery (1998) was a source of numerous characters. The characters and character states are listed and discussed below. The data matrix is presented in Table 3.6.1.

Apical system

1. Number of gonopores in the apical system: four (0); three (1). Most micrasterids have four gonopores in their apical system, but *Cyclaster* and *Isaster* differ in having only three. In both genera it is genital plate 2 that lacks a gonopore.

2. Position of apical disc as a percentage of test length from the anterior margin: <40 (0); >40 (1).

Anterior ambulacrum

3. Anterior ambulacrum: petaloid (0); apetaloid (1). Some micrasterid taxa have elongate pores in the anterior ambulacrum, but in others (e.g. *Micraster*) the pores are round meaning that these taxa lack an anterior petal.

4. Anterior margin: convex (0); flat to slightly notched (1); distinctly notched (2).

Paired ambulacra

5. Divergence of anterior paired petals: <100° (0); 100-120° (1); >120° (2).

6. Length of anterior paired petals as a percentage of the length to the ambitus: <40 (0); 40-60 (1); >60 (2).

7. Length of posterior paired petals as a percentage of the length to the ambitus: <35 (0); 35-48 (1); >48 (2).

8. Relative length of anterior to posterior paired petals: <1.2 (0); >1.2 (1).

9. Sunkeness of petals: virtually flush (0); noticeably depressed (1).

10. Pores in paired petals: small and circular (0); circular anteriorly and elongate posteriorly (1); elongate (2).

11. Width of poriferous zone: narrower than interporiferous zone (0); equal in width to interporiferous zone (1); wider than interporiferous zone (2).

Peristome and Periproct

12. Peristome: facing downwards (0); facing forwards (1).

13. Mouth: >15% of test length from the anterior margin (0); <15% of test length from the anterior margin (1).

14. Extent of labral projection as a percentage of mouth length: <33 (0); 33-99% (1) ≥100% (2).

15. Peristome rim: absent or weak (0); prominent (1).

16. Width of mouth as a percentage of test width: <16% (0); >16% (1).

17. Periproct: high (0); low (1).

Plaston and interambulacra

18. Plastron: asymmetrical (0); symmetrical (1). In some taxa (e.g. *Plesiaster*) the two sternal plates are unequal in size with an oblique suture running between them, in others (e.g. *Micraster*) the plates are symmetrical with a vertical suture.

19. Posterior interambulacrum on upper surface: non-carinate (0); carinate (1).

20. Relative length to width of labral plate: <2.5 (0); >2.5 (1).

21. Shape of labral plate: not tapered posteriorly (0); tapered posteriorly (1).

Fascioles and tuberculation

22. Subanal fasciole: absent (0); present (1). While this character has been used to define the micrasterids, it is absent in some taxa (e.g. *Isaster*).

23. Peripetalous fasciole: absent (0); incomplete (1); complete (2). Most micrasterids lack a peripetalous fasciole, but a few (e.g. *Cyclaster pfenderae*) have well developed peripetalous fascioles. Other taxa have peripetalous fascioles that are present only as series of aligned bands (e.g. *Plesiaster peini*) or that do not form a complete loop (e.g. *Cyclaster galei*); in both these cases the taxon is coded as having an incomplete fasciole.

24. Peripetalous fasciole: absent (0); incomplete (1); complete (2).

25. Tuberculation: normal (0); pustular (1).

Overall test shape

26. Width of test as a percentage of length: <75 (0); >75 (1).

27. Shape in plan view: rectangular (0); tapered (1); ovate (2).

28. Height as a percentage of test length: <55 (0); >55 (1).

29. Lower surface: approximately flat (0); inflated (1)

Epiaster breyniusi	01021	21112	10000	00000	00000	1100
Plesiaster peini	01022	22112	00010	00000	01010	1110
Plesiaster hourcqi	01022	22112	00110	00100	01010	1110
Plesiaster nobilis	01022	22112	00010	00100	01010	1110
Plesiaster trangahyensis	01122	22112	00010	00100	01010	1110
Plesiaster amnicus	01122	22112	00?10	00000	01010	1110
Cyclaster galei	11100	00000	00011	10100	11210	0000
Cyclaster grindrei	10122	10102	20000	00111	012?0	1110
Cyclaster heberti	11111	11112	20011	00111	11220	1100
Cyclaster integer	11111	11001	10010	10111	11220	1110
Cyclaster pfenderae	11101	11112	20001	00100	01221	1210
Cyclaster platornatus	11100	00112	20001	10100	01221	1200
Cyclaster ruegensis	11101	00000	000?0	00100	01200	1000
Cyclaster vilanovae	11111	11012	20000	10111	11210	1110
Isaster acquitanicus	11002	11102	20001	01100	00000	1210
Gibbaster gibbus	01022	22112	21120	01101	11100	1120
Gibbaster senonensis	01022	22112	21120	01101	10100	1120
Micraster coranguinum	01121	22112	01120	00111	11000	1110
Diplodetus nutrix	01122	11112	01010	10110	01011	0100
Diplodetus duponti	01121	11112	01011	10110	01011	0100
Diplodetus bucardium	01122	11112	01010	10110	01011	0100
Diplodetus americanus	01121	11112	01010	10111	01011	0100
Diplodetus parvistella	01121	11112	01010	10110	01010	0100
Diplodetus coloniae	00122	11012	01010	10010	01010	0100
Diplodetus gauthieri	01121	11012	01010	10110	01010	0100
Ovulaster zignoi	00112	???00	00100	00101	?1100	0121
Ovulaster auberti	00112	???00	00100	00101	?1100	1121
Ovulaster reticulatus	00112	???00	00100	00101	?1100	0120
Turanglaster nazkii	01112	???00	?0100	0010?	?1000	1121

Table 3.6.1: Data matrix used in the phylogenetic analysis of the micrasterids.

3.6.4 RESULTS AND DISCUSSION

The heuristic search produced 543 MPTs of 103 steps (CI = 0.388; RI = 0. 711). The strict consensus tree is presented in figure 3.6.1 and the 50% majority rule tree in figure 3.6.2. In the strict consensus tree the micrasterids are divided into three distinct clades, the interrelationships of which are unresolved. The first consists of *Micraster*, *Gibbaster*, *Ovulaster* and *Turanglaster* and consists of two sub-clades, one containing *Micraster* and *Gibbaster* and the other containing *Ovulaster* and *Turanglaster*. The second contains the genus *Diplodetus* and the third contains *Cyclaster* with *Isaster acquitanicus* falling within the *Cyclaster* species. In addition to these three

clades are a group of *Plesiaster* species whose relationships are poorly resolved in the strict consensus tree.

In the 50% majority rule tree there are two major clades. Firstly, a clade containing the *Cyclaster* plus *Isaster* clade and the *Diplodetus* clade, and, secondly, a clade containing the remaining taxa. In this latter clade the *Plesiaster* species form a paraphyletic basal group to the *Micraster* plus *Gibbaster* plus *Ovulaster* plus *Turanglaster* clade.

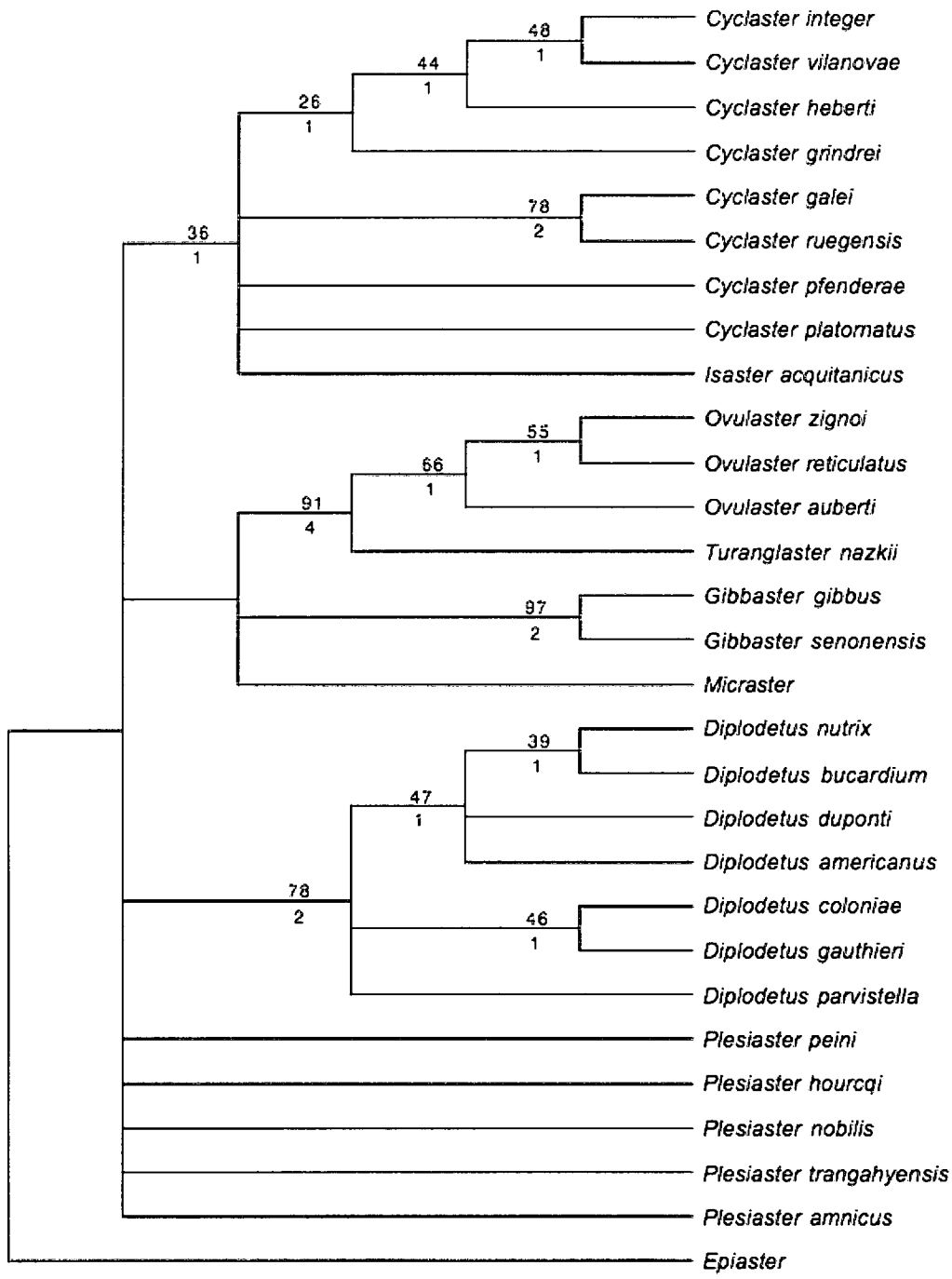

Figure 3.6.1: Strict consensus tree of micrasterid species. Bootstrop support values are displayed above the branch leading to each node and decay indices are displayed below.

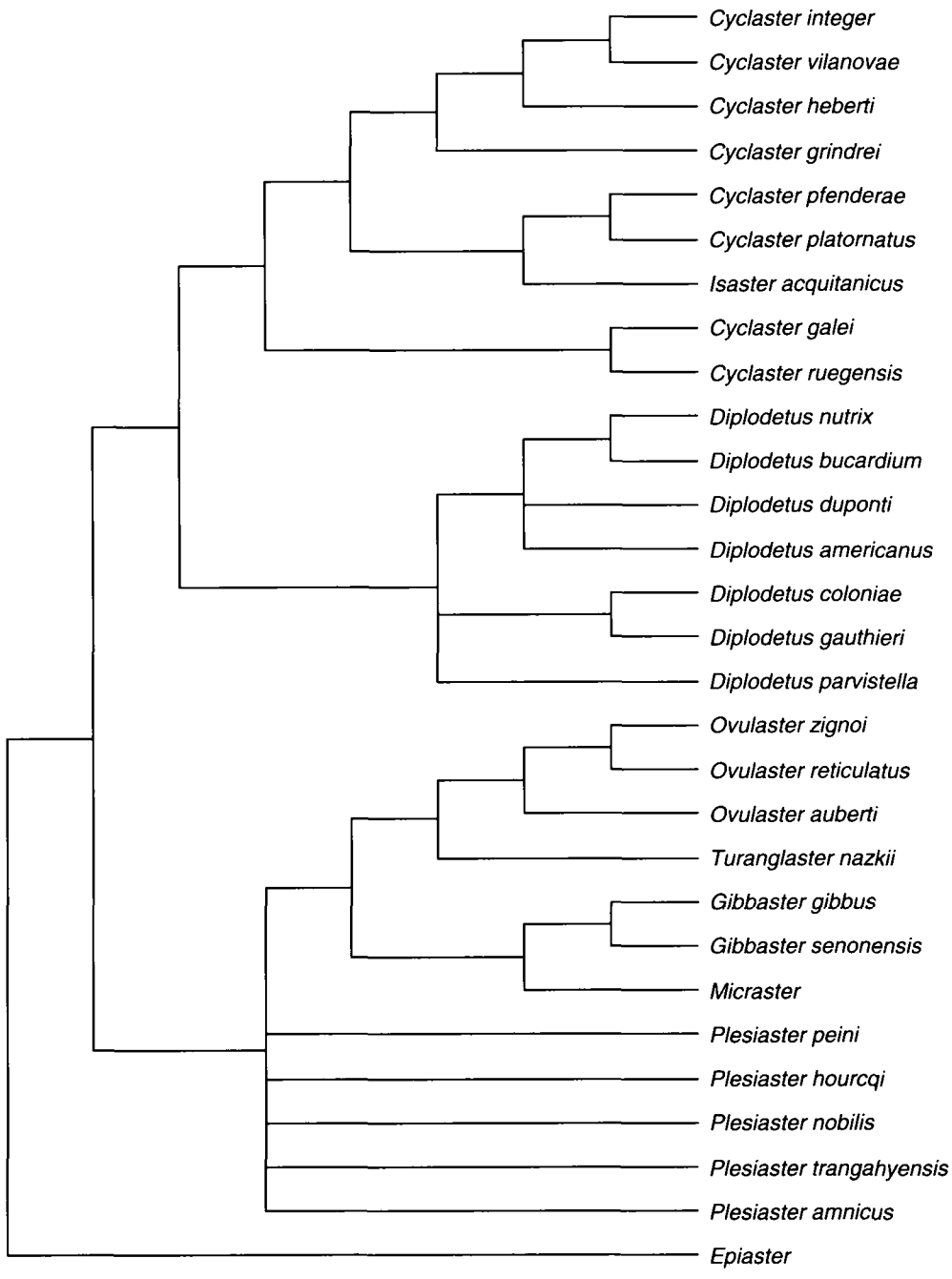

Figure 3.6.2: 50% majority rule consensus tree for micrasterid species.

3.7 PALEOPNEUSTOIDEA

To date there has been little detailed analysis of the interrelationships of the Paleopneustina and, as Stockley *et al.* (2005) noted, denser sampling of this portion of the spatangoid tree is needed in order to resolve the questions posed by the difference in phylogeny recovered by molecular and morphological methods. As there are only three Cretaceous paleopneustid species in two genera, no species level analysis of this group is undertaken. Here I have carried out a species level analysis of the Schizasteridae.

3.7.1 TAXA AND OUTGROUP

I have, to my knowledge, included all Cretaceous species of Schizasteridae whose morpholology is sufficiently well known to be included in the data matrix. Taxa considered to be hemiasterids at the *bifasciata* stage are excluded from the analysis, as they are considered to be hemiasterids. *Polydesmaster fourtaui* was used as the outgroup for the analysis. The genus *Polydesmaster* [=*Mundaster*] has previously been considered to be allied with the toxasterids (see Villier *et al.* 2004), but was found to lie basally to the schizasterid spatangoids by both Villier *et al.* (2004) and Stockley *et al.* (2005) as well as in the genus level anaysis in this thesis; it may lie within the stem group of Paleopneustina (Smith 2005).

3.7.2 ANALYTICAL METHODS

The analytical methodology used in this analysis is the same as that used in the analysis of hemiasterid species, but with the exception that the results were presented on the 50% majority rule tree, rather than the strict consensus tree.

3.7.3 CHARACTER CODING AND DEFINITIONS

Each species was coded for 11 morphological characters. Many of these characters were derived or modified from previous phylogenetic analyses of spatangoid taxa, especially Villier *et al.* (2004), Stockley *et al.* (2005) and

Jeffery (1997, 1998). The characters are listed and discussed below. The data matrix is presented in Table 3.7.1.

Apical System

1. Position of apical disc: anterior (<40% test length from anterior) (0); central (40-60% of test length from anterior) (1); posterior (>60% test length from anterior) (2).

2. Apical disc plating: ethmophract (0); semi-ethmolytic (1); ethmolytic (2). While this character has been considered to be very important in high-level spantangoid taxonomy with schizasterids characterized by having an ethmolytic apical system, all three states are present in taxa assigned to the schizasterids.

Anterior ambulacrum

3. Length to width ratio of plates in anterior ambulacrum: more than five times broader than high (0); 1.5 to 5 times as wide as high (1); approximately as broad as high (2).

4. Maximum breadth of anterior ambulacrum: narrower or equal to paired ambulacra (0); wider than paired ambulacra (1).

Paired ambulacra

5. Relative lengths of anterior and posterior petals (equipetality): posterior pair at least 80% length of anteriors (0); posteriors 50-80% length of anteriors (1) posteriors <50% length of anteriors (2).

Interambulacral plating and plastron

6. Shape of labral plate: broadens posteriorly (0); narrows posteriorly (1). In many spatangoids the labral plate widens to the posterior but schizasterids tend to have a T-shaped labrum that is widest at the anterior margin.

7. Length to width ratio of labral plate: <1.2 (0); 1.2-3.1 (1); >3.1

8. Length of labral plate relative to that of sternal plates: <20% (0); 20-50% (1); >50% (2). Stockley *et al.* (2005) used this character and treated it as ordered in their analysis.

Test shape

9. Posterior keel: absent or rounded (0); sharp (1); all interambulacra keeled (2). In some taxa the posterior interambulacrum forms a sharp keel running between the apical disc and the periproct (e.g. *Schizaster chargensis*), while in others this region is gently rounded (e.g. *Periaster elatus*). In a few species all interambulacra have sharp keels (e.g. *Schizaster variabilis*).

10. High point: central (0); posterior (over 25% of test length behind the apical system) (1). In most taxa the highest point of the test lies approximately centrally, but in a few it is positioned posteriorly.

11. Posterior truncation of test: oblique (0); vertical (1); overhanging (2).

Polydesmaster fourtaui	0100?	??001	0
Periaster elatus	1001?	?0000	0
Periaster undulatus	11011	00010	1
Periaster ciryi	11011	00011	0
Linthia brodermanni	02100	11000	0
Linthia sudanensis	12100	01000	0
Linthia payeni	02?0?	?1000	0
Schizaster chargensis	1212?	?0110	1
Schizaster indicus	12121	00010	1
Schizaster joannisboemeni	12(12)1?	??111	1
Schizaster sindensis	1211?	?0000	1
Schizaster variabilis	1212?	?0200	1
Tessieria senegalensis	12111	1?000	1
Abatus pseudoviviparus	0211?	?0000	0

Table 3.7.1: Data matrix used in the phylogenetic analysis of the schizasterids.

3.7.4 RESULTS AND DISCUSSION

The branch and bound search produced 111 trees of length 23 (CI = 0.609; RI = 0.700). The 50% majority rule consensus tree is presented in Figure 3.7.1. *Periaster* froms a paraphyletic group at the base of the tree. This result is in line with previous schemes for the early evolution of the schizasterids (e.g Néraudeau *et al.* 2003). More work is required to understand precisely how the schizasterid clade originated from within the hemiasterids. The remaining taxa form two clades: in the first *Abatus* forms the sister group to *Linthia*; and in the second *Tessieria* forms the sister group to *Schizaster*. The relationships between the schizasterids and the other paleopneustid clade, the prenasterids, are examined in the discussion of the genus level analysis in Section 3.3.

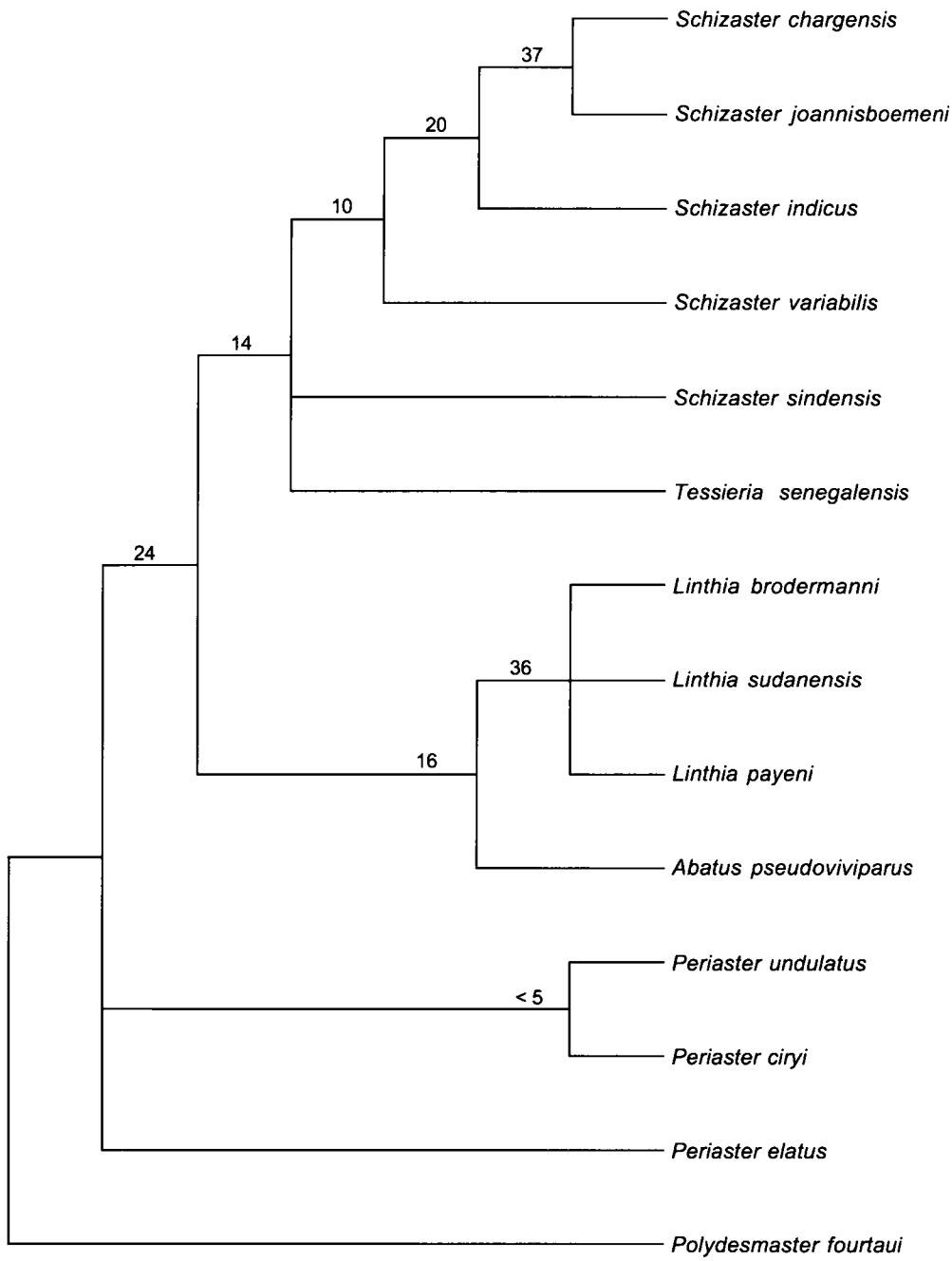

Figure 3.7.1: 50% majority rule tree for the schizasterids. Bootstrap support values are shown above the branch leading to each node. No nodes have Bremer support values of greater than 1.

3.8 SOMALIASTERIDAE

The phylogenetic position of this family within atelostomates has been problematic because the included taxa share not only a compact apical system and depressed petals (typical of spatangoids), but also a meridosternous plastron (typical of holasteroids). Authors have variously assigned somaliasterid taxa to both groups (see table 1 of Jeffery 1999). Jeffery (1999) used phylogenetic analysis to determine the position of somaliasterids within the atelostomates, concluding that they are in fact spatangoids. Despite this work, there has hitherto been no comprehensive analysis of the interrelationships of the somaliasterid species. Here I address this issue by extending the analysis of Jeffery (1999) to include all sufficiently well known somaliasterid species.

3.8.1 TAXA AND OUTGROUP

I include all described species of somaliasterid except *Iraniaster nodulosus*, which is too poorly known to be included. I have included the two exclusively Palaeocene species (*Brightonia macfadyeni* and *Leviechinus gregoryi*) for completeness. *Mauritanaster gentili* was used as the outgroup because Jeffery (1999) found this taxon to form the immediate sister group to the somaliasterids.

3.8.2 ANALYTICAL METHODS

The methodology used for this analysis is identical to that used in the phylogenetic analysis of aeropsid species outlined in section 3.4.2, with the following exceptions: (1) an exhaustive (rather than branch and bound) search was used because the small size of the dataset made this possible; and (2) the bootstrap and Bremer support values were displayed on the single most parsimonious tree rather than a consensus tree.

3.8.3 CHARACTER CODING AND DEFINITIONS

The characters and coding largely follow Jeffery (1999). Three additional taxa are coded (*Iraniaster affinidouvillei*, *I. affinimorgani* and *I. bowersi*) and the non-somaliasterid taxa are excluded except for the outgroup *Mauritanaster gentili*. One additional character (character 25) is added. Some characters become uninformative or constant when the non-somaliasterid taxa are removed, these characters are retained, but the CI is recorded both with and without these characters included. The characters and character states are outlined below. The data matrix is presented in Table 3.8.1.

1. Number of gonopores: four (0); three (1); two (2).

2. Supplementary gonopores in ocular plates: absent (0); present (1).

3. Apical system: elongate (0); compact (1).

4. Apical system: posterior genital plates in contact (0); madreporite separates posterior genital plates (1).

5. Apical system: posterior ocular plates in contact (0); madreporite separates posterior ocular plates (1).

6 Apical system: posterior ocular plates in contact with posterior genital plates (0); posterior ocular plates disjunct from posterior genital plates (1).

7. Marginal fasciole (below anus): absent (0); present (1).

8. Peripetalous fasciole (above anus): absent (0); present (1).

9. Subanal fasciole: absent (0); present (1).

10. Latero-anal fasciole: absent (0); present (1).

11. Number of interambulacral plates adjoining labrum: one (0); two (1).

12. Labral and sternal plates: in contact (0); disjunct (1).

13. Angle between line through mouth and anus and suture between first and second post-labral interambulacral plates: <40° (0); 40–90° (1).

14. First and second post-labral interambulacral plates (i.e. plates 2b and 2a): not symmetrical (0); symmetrical (1).

15. Second and third post-labral interambulacral plates (i.e. plates 2a and 3b): not symmetrical (0); symmetrical (1).

16. First and second post-labral interambulacral plates (i.e. plates 2b and 2a): not equal sized (0); equal sized (1).

17. Second and third post-labral interambulacral plates (i.e. plates 2a and 3b): not equal sized (0); equal sized (1).

18. Paired ambulacra: non-petaloid (0); sub-petaloid (1); petaloid (2).

19. Paired ambulacra: flush (0); sunken (1).

20. Paired ambulacra: non- or sub-petaloid (0); parallel-sided (1); bowed (2).

21. Pore shape in paired ambulacra: round in both columns (0); anterior and posterior columns differentiated (1); elongate in both columns (2).

22. Width of poriferous zone: non-petaloid (0); narrower (1); broader than zone between (2).

23. Relative length of posterior to anterior petals: non- or sub-petaloid (0); > 0.8 (1); < 0.8 (2).

24. Percentage length of anterior paired petals to ambitus: non- or sub-petaloid (0); < 85 per cent. (1); > 85 per cent (2).

25. Height of the periproct: mid-height or above (0); below mid-height (1).

Mauritanaster gentili	00111	00100	10010	10211	2212
Brightonia macfadyeni	20100	00100	01000	10211	2212
Iraniaster douvillei	00110	00100	00100	01211	2212
Iraniaster morgani	00110	00100	0?100	01211	2212
Iraniaster omanensis	00111	00100	01000	10211	2212
Iraniaster bowersi	00110	00100	00100	00211	22?2
Iraniaster affinidouvillei	00110	00100	00100	01211	2212
Iraniaster affinimorgani	00110	00100	00000	00211	2212
Leviechinus gregoryi	20111	00100	01000	10211	2212

Table 3.8.1: Data matrix used in the phylogenetic analysis of the somaliasterids.

3.8.4 RESULTS AND DISCUSSION

The exhaustive search produced a single MPT of 11 steps with CI 0.909 (0.875 with uninformative characters removed) and RI 0.929; this is presented in figure 3.8.1.

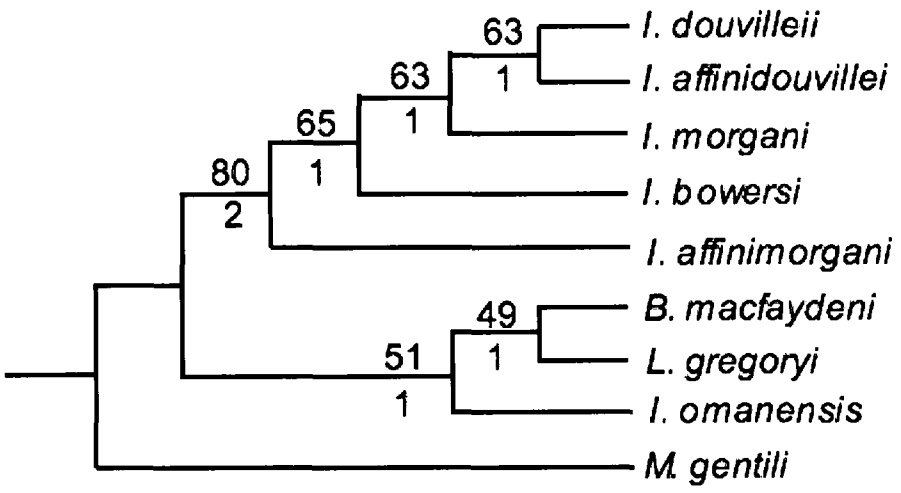

Figure 3.8.1: The single most parsimonious tree. Bootstrap values are displayed above each node and Bremer support values below.

The various species of *Iraniaster*, apart from *I. omanensis*, form a well-supported clade with a bootstrap value of 80 and a decay index of 2. *Iraniaster omanensis* lies at the base of a second clade which also contains the Palaeocene genera *Leviechinus* and *Brightonia*. There is, therefore, a case for excluding *I. omanensis* from the genus *Iraniaster* and assigning it instead to a new genus. However, the clade containing *I. omanensis* is not very strongly supported (bootstrap 51; decay index 1) and a tree in which all species of *Iraniaster* form a monophyletic clade is only a single step longer than the MPT. Furthermore, a Templeton's test shows that the MPT is not a significantly better explanation of the data than one with a monophyletic *Iraniaster* clade (p=0.3173). I thus retain this species in the genus *Iraniaster*.

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4. THE TIMING AND LOCATION OF SWITCHES TO NON-PLANKTOTROPY

4.1 INTRODUCTION

In spite of the widespread and growing interest in the interplay between evolutionary and developmental processes (see Chapter 1), we still know relatively little about the evolutionary history of larval development. In many clades multiple shifts from planktotrophic development to non-planktotrophic development have been inferred by mapping larval modes onto phylogenetic trees (e.g. echinoids (Wray 1992; Smith *et al.* 1995); temnopleurid echinoids (Jeffery & Emlet 2003; Jeffery *et al.* 2003); asterinid starfish (Hart *et al.* 1997); *Conus* gastropds (Duda & Palumbi 1999); littorinid gastropods (Reid 1989); turritellid gastropods (Lieberman *et al.* 1993)). An important, and yet much overlooked, issue is when and where these switches to non-planktotrophy occurred: were shifts to non-planktotrophy scattered randomly through time and space, or were they concentrated temporally or spatially? The question is important as it may help to elucidate the factors that drive shifts to non-planktotrophy. If the switches were concentrated in particular time intervals or spatial zones then this would imply that extrinsic factors operating at these times or in these places are responsible for driving the switches to non-planktotrophy.

The tacit assumption among biologists seems to be that the switches were scattered randomly throughout geological history (Jeffery 1997). However, when Jeffery (1997) carried out a broad survey of all major echinoid clades she found near synchronous switches to non-planktotrophy in five different orders in the latest Cretaceous, with no examples of non-planktotrophy known from earlier than this interval. Despite this study, we still know little about the finer scale patterns within orders and at lower taxonomic levels. Here I address this question by focussing on a single order, the Spatangoida.

Much has been written about the spatial distribution of planktotrophic and non-planktotrophic taxa. Thorson (1950) argued that brooded taxa predominated in polar and deep-water regions as a result of a lack of an adequate planktonic food supply (all planktonic larvae were believed to be planktotrophic at the time he wrote); this concept has later become known as 'Thorson's rule' (Mileikovsky 1971). Thorson's rule became widely accepted and many groups have been cited as examples that follow Thorson's rule (see references in Poulin & Feral 1996) and it has formed the basis of mathematical models of larval selection (see Pearse 1994 for review). However, while many high latitude taxa are non-planktotrophic, many of these are now known to be planktonic non-planktotrophs rather than brooders (Bosch & Pearse 1990; Pearse *et al.* 1991; Pearse 1994; Hain & Arnaud 1992). Thus, although Thorson's model, which is based solely on feeding, may explain the increase in non-feeding larvae at high latitude, it can be criticized for its failure to explain why brooding (in addition to planktonic non-planktotrophy) is particularly abundant in Antarctic waters (e.g. Pearse & Lockhart 2004).

One way in which the abundance of Antarctic brooders has been explained is that brooding taxa experienced lower levels of extinction during the coolest parts of the Cenozoic (Poulin & Feral 1996; Poulin *et al.* 2002). Poulin *et al.* (2002) argued that at these times extensive ice cover would have reduced the amount of light reaching the sea surface and hence the primary productivity would have declined, potentially leading to the extinction of clades of taxa with planktonic larvae. Thus, according to the model of Poulin *et al.* (2002), the preponderance of brooders in Antarctic waters is a reflection of species selection that operated in the past rather than selection for current environmental conditions. Poulin *et al.* argue that selection for current conditions is an unlikely cause because, while there are fewer planktonic species in the Antarctic today, planktonic taxa are dominant in

terms of number of individuals.

In this study I take a different approach and, rather than assessing the spatial distributions of taxa employing different larval modes at the present day (or any other point in time), I try to establish where shifts to non-planktotrophy first evolved within the spatangoid sea urchins. To do this I have identified the locations of the first known occurrences of non-planktotrophic clades in the fossil record. This approach enables us to establish whether there is any pattern in the location of these switches, for example one might expect to find that swiches to non-planktotrophy occurred preferentially in high latitude regions (although Jeffery (1997) did not identify such a pattern in the major sea urchin clades).

4.2 MATERIALS AND METHODS

This study focuses on the Cretaceous spatangoid sea urchins. The group is ideal for this study for a number of reasons (see also Section 1.3.2): (1) they are unusual in that larval strategy can be inferred from the adult test using either morphological criteria or apical disc crystallography (see below); (2) they are commonly preserved and the apical system is usually present, meaning that there is abundant suitable material for analysis; (3) they lived in a wide variety of environments and from the equator to the poles, so they can used to assess whether these factors correlate with switches in larval mode; (4) their complex morphology makes it relatively straightforward to establish their evolutionary relationships; and (5) the group contains both planktotrophic and non-planktotrophic taxa and spans the time when non-planktotrophy is thought to have first evolved within the group.

4.2.1 Inference of larval modes

The larval modes of 111 fossil spatangoid specimens from museum collections were analysed (presented in Appendix 2). Three criteria were

used for inferring the mode of larval development from adult fossil sea urchin specimens:

(1) Identification of brood pouches (marsupia). Some non-planktotrophic taxa brood their larvae and a subset of these do so in specialized brood pouches on the test of the female; the identification of such marsupia is indicative of non-planktotrophic development (e.g. Kier 1969).

(2) Extreme sexual dimorphism of gonopore size. Because non-planktotrophic taxa have much larger eggs (Emlet *et al.* 1987; Emlet 1989, 1995) the females frequently have enlarged gonopores through which to extrude these eggs. Extreme sexual dimorphism can indicate non-planktotrophic development (Emlet 1989).

(3) Crystallographic orientation of the apical plates. The crystallographic method for determining larval mode has been described by Emlet (1985, 1989). In the past applying this method involved physically sectioning the specimen. However, it is now possible to carry out this technique non-destructively by decorating the plates of the apical system with microscopic calcite crystals grown in optical continuity with the plates (Okazaki *et al.*, 1981), each of which behaves as a single crystal. This methodology, and the protocol used in this thesis, will be described here.

The method relies on the fact that the planktotrophic larva has skeletal calcite rods, the main function of which is to support the larval arms that are used in feeding; during metamorphosis some of the apical plates grow from the proximal ends of the rods imparting a characteristic crystallographic orientation to the plates. In non-planktotrophic larvae these rods are absent and the apical plates all form *de novo* at metamorphosis, producing a distinct pattern of c-axis orientations.

(a) Crystal decoration

The c-axis orientations can be calculated from the orientations of the face poles, which can be identified by 'flashes' (similar in appearance to sunlight glinting from a window) when looking at the plate in this orientation. In some specimens these 'flashes' could be readily observed without decoration. In most specimens, however, it was necessary to grow calcite in optical continuity with the plates in order to observe these 'flashes'. In order to do this, the following protocol, developed by Okazaki *et al.* (1981), was followed:

- Place specimen apex down in 0.01% acetic acid for ten minutes to provide a fresh surface for crystals to grow on.
- Place in a 0.1 molar solution of sodium hydroxide for five minutes to neutralize.
- Rinse in tap water.
- Place apex down in a 5:2 mixture of 0.1 molar sodium hydrogen carbonate and 0.1 molar calcium chloride for 30-60 minutes.
- Rinse in ethanol to prevent thick build-ups of calcite.

In some specimens it was necessary to repeat this process several times before 'flashes' could be observed.

(b) Determination using an optical goniometer

When 'flashes' were observed the specimen was then placed on an optical goniometer in order to determine the orientations of the face poles. The goniometer allows the specimen to be rotated in two planes that are perpendicular to one another. The specimen was rotated until 'flashes' were observed and the orientation in each plane was noted.

(c) Calculating c-axes with CALCAXES

The computer programme CALCAXES (Fisher & Bodenbender 1993) can be used to calculate the c-axes orientations from face pole orientation data. It can also be used to predict the orientation of the remaining face pole, given

the orientations of two observed face poles. This latter function should be used sparingly, as there is a danger that objectivity may be reduced if a very weak 'flash', that would otherwise be ignored, is recorded as a face pole because it coincides with an orientation suggested by CALCAXES. In order to maximize objectivity, the following protocol was used in this thesis:

- The possible orientations were explored in a systematic way and the orientations of any 'flashes' were recorded.
- If face poles remained to be found, the programme CALCAXES was used to predict their orientations and the suggested orientations were checked.
- In order to increase accuracy and confidence in the results, attempts were made (using CALCAXES if necessary) to find two readings for each face pole. This results in a total of six readings for each genital plate.

(d) Plotting c-axes with STEREONET

The computer programme STEREONET v. 6.3 X (Allmendinger 2005) was used to plot the c-axes onto stereonets. In irregular echinoids the convention (Emlet 1989) is to plot the c-axes onto a stereonet where north represents axes dipping towards the anterior of the animal, east represents points dipping towards the right of the specimen when viewed from above, and so on. Points that plot close to the centre of the stereonet correspond to c-axes which lie at a high angle to the plane of the apical system, those that lie far from the centre represent c-axes orientated at a low angle to the plane of the apical system.

(e) Identification of larval modes

The criteria for recognizing planktotrophic and non-planktotrophic larval development have been established by Emlet (1989) based on observations of a large number of extant species with known larval mode. For irregular echinoids Emlet observed that the c-axes of plates G4, G2 and G3, which

form from larval calcite rods, tend to lie in a line from the centre to the bottom left of the stereonet (though in this work it was noted plate G2 often plotted some distance above this line); plate G1 which forms *de novo* lies close to the centre of the stereonet (See Figure 4.1). In non-planktotrophs, on the other hand, all plates form *de novo* at metamorphosis and their c-axes all plot close to the centre of the stereonet. In this thesis specimens were inferred to have planktotrophic development if the c-axes of plates G2 and G3 plotted in the bottom left quadrant with G3 outside the 45° circle and closer to the edge of the stereonet than G2. If all plates fell inside the 45° circle then specimens were inferred to have had non-planktotrophic development. Specimens exhibiting any other patterns of c-axis orientations were determined to have unknown developmental mode.

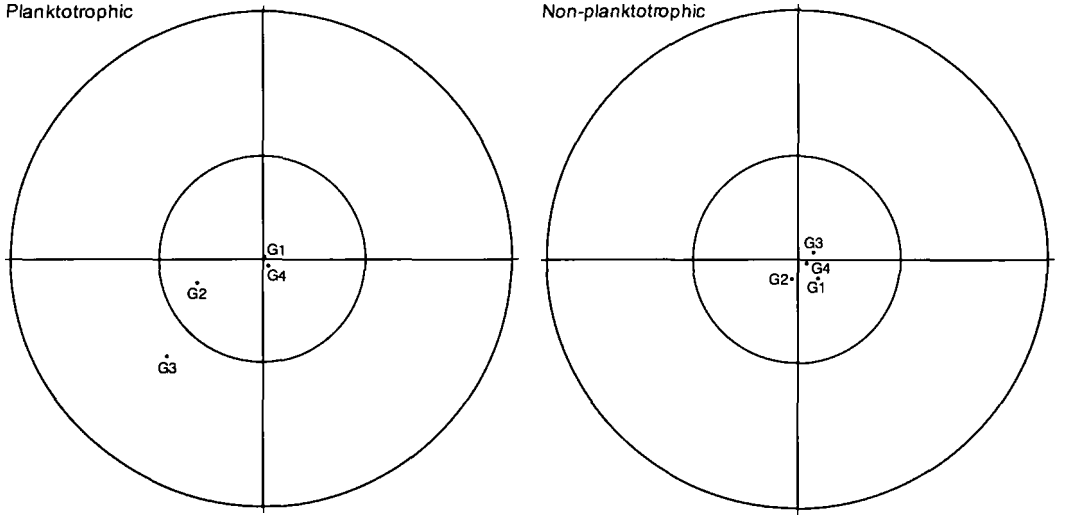

Figure 4.1: The characteristic c-axis orientations of genital plates in planktotrophic and non-planktotrophic spatangoids, see text for explanation. The planktotrophic speciemen is *Mecaster nicaisei* (MNHN L22329); the non planktotrophic specimen is *Mauritanaster mirabilis* (MNHN L22318).

Specimens in which sexual dimorphism of gonopore size was present, but crystallographic analysis produced patterns of c-axis orientations typical of planktotrophic taxa were interpreted as planktotrophs. This is because Emlet's (1989) study of gonopore size in extant species of known larval mode revealed that some degree of dimorphism can occur in planktotrophic

species. On the other hand, Emlet (1989) found that crystallographic orientations could consistently distinguish between planktotrophy annd non-planktotrophy.

4.2.2 Phylogenetic analysis

An understanding of phylogenetic relationships is needed in order to assess the number, direction and timing of shifts in larval mode. This study uses the genus level analysis of Section 3.3 as a basis for studying these shifts.

4.2.3 Determination of the number, timing and location of switches

The inferred larval modes were mapped onto the novel phylogeny of the group. This allowed determination of the number and direction of switches in developmental mode within the group. This information was combined with the stratigraphic ranges of the taxa to enable elucidation of the timing of these shifts in developmental mode. The localities of the first occurrences of each of the non-planktotrophic clades in the fossil record were plotted onto a palaeogeographic reconstruction for the Maastrichtian (Ziegler & Rowley 1998) in order to ascertain the location of the switches to non-planktotrophic development. This will introduce some error as the continents will have shifted between the time of the first switches in the Campanian and those that occurred in the Maastrichtian. However, the continental movements, and hence the errors, involved are relatively small.

Table 4.1: Larval modes of Cretaceous spatangoid genera. Ber = Berriasian, Val = Valanginian, Haut = Hauterivian, Bar = , Apt = Aptian, Alb = Albian, Cen = Cenomanian, Tur = Turonian, Sant = Santonian, Camp = Campanian, Maas = Maastrichtian, 'Sen' = 'Senonian', Ter = Tertiary, Rec = Recent.

Genus	Crystallographic Signature	Marsupia?	Gonopore dimorphism?	Stratigraphic range
Toxaster	Planktotrophic	No	No	Val-Apt
Heteraster	Planktotrophic	No	No	Bar-Cen
Mokotibaster/ Niponaster	Planktotrophic	No	No	Maas/'Sen'
Macraster	Planktotrophic	No	No	Alb-Cen
Epiaster	Planktotrophic	No	No	Bar-Alb
Pliotoxaster	Planktotrophic	No	No	Apt-Cen
Iraniaster	Planktotrophic	No	No	Camp-Maas
Palhemiaster	Planktotrophic	No	No	Apt-Alb
Mecaster	Planktotrophic	No	No	Cen-Maas
Lambertiaster	Planktotrophic	No	No	Camp-Maas
Holcopneustes	Planktotrophic	No	No	Maas-(Ter)
Polydesmaster	?	No	No	Cen-Tur
Periaster	Planktotrophic	No	No	Cen-Con
Abatus	?	Yes	Yes	Maas-(Rec)
Linthia	Planktotrophic	No	No	Camp-(Ter)
Schizaster	Planktotrophic	No	No	UCamp-(Ter)
Tessieria	?	No	No	Maas
Holanthus	Planktotrophic	No	No	Maas-(Rec)
Leiostomaster	Non-planktotrophic	Yes?	Yes	'Sen sup.' (?Camp) – (Rec)
Bolbaster	Planktotrophic	No	No	U.Cret-(Ter)
Hemiaster	Planktotrophic	No	No	Alb-Maas
Leymeriaster	Planktotrophic	No	Yes	Cen-Maas

Proraster	Planktotrophic	No	No	Camp-(Ter)
Mauritanaster	Non-planktotrophic	No	Yes	Maas-(Ter)
Heterolampas	Non-planktotrophic	No	Yes	Camp
Plesiaster	Planktotrophic	No	No	Sant-(Ter)
Diplodetus	Non-planktotrophic	Yes?	Yes	Camp-(Ter)
Gibbaster	Planktotrophic	No	No	Tur-Camp
Isaster	Planktotrophic	No	No	Maas-(Ter)
Cyclaster	Non-planktotrophic	No	Yes	Camp-(Rec)
Micraster	Planktotrophic	No	No	Tur-(Ter)
Turanglaster	?	No	No	Camp
Ovulaster	Planktotrophic	No	No	Con-(Ter)
Homoeaster	Planktotrophic	No	No	Con-(Ter)
Orthaster	Planktotrophic	No	No	Camp-(Ter)
Cottreaucorys	Planktotrophic	No	No	Maas-(Ter)
Coraster	Planktotrophic	No	No	Maas-(Ter)

4.3 RESULTS

Larval modes of Cretaceous spatangoid taxa

Crystallographic analysis was attempted for 111 specimens, and larval mode was successfully inferred for 73 of these; the specimens analysed, as well as 20 additional specimens analysed by Jeffery (1997) and Emlet (unpublished) are listed in Appendix 2. Table 4.1 contains a summary of the data on crystallographic orientations, gonopore dimorphism and the presence or absence of marsupia for each of the Cretaceous spatangoid genera, as well as listing the stratigraphic ranges of the genera.

Timing of switches to non-planktotrophy

The data on larval modes inferred from morphological and crystallographic criteria were mapped onto the phylogeny of Cretaceous spatangoids, which is plotted against the geological timescale in Figure 4.2. These results reveal that non-planktotrophic development arose independently five times within the Cretaceous spatangoids. All five non-planktotrophic clades first appear in the fossil record in either the Campanian or Maastrichtian. The known ranges of taxa exhibiting non-planktotrophy extend no further back in time than the early Campanian and planktotrophy is the only strategy observed prior to this. The Campanian to Maastrichtian is also the interval during which the first known instance of non-planktotrophy in four other echinoid orders has been recorded; there are no reported occurrences of non-plantotrophy in echinoids from any earlier than this time (Jeffery 1997). (Though sexual dimorphism has been reported from earlier in the Cretaceous (Smith 1988; Néraudeau 1993), in both cases Emlet (pers. comm. to Jeffery 1997) has shown using crystallographic analysis that these taxa are planktotrophic.)

Location of switches to non-planktotrophy

The first occurrence of each of the non-planktotrophic clades identified are plotted onto the palaeogeographic reconstruction of Ziegler & Rowley (1998)

and presented in Figure 4.3. All non-planktotrophic clades make their first appearance in the fossil record in temperate or sub-tropical latitudes. Thus, in common with Jeffery's (1997) work on all echinoid clades, this study does not find evidence for preferential origin of non-planktotrophic clades at high latitude. This is in contrast to the modern distribution of larval modes where non-planktotrophic development is unusually common in polar latitudes (e.g. Pearse & Lockhart 2004).

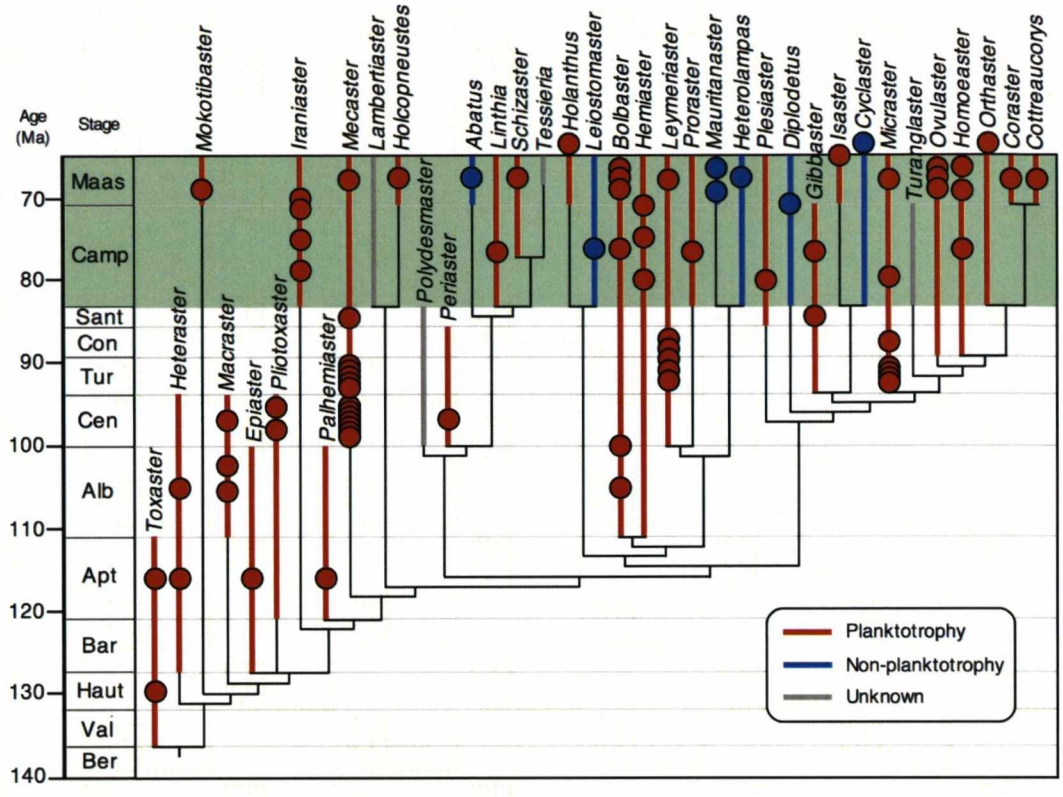

Figure 4.2: Strict consensus tree of Cretaceous spatangoid genera plotted against the geological timescale. Planktotrophic taxa are shown in red, non-planktotrophic taxa in blue and unknown development in grey. Coloured circles represent specimens for which development has been inferred. Green band highlights the Campanian-Maastrictian.

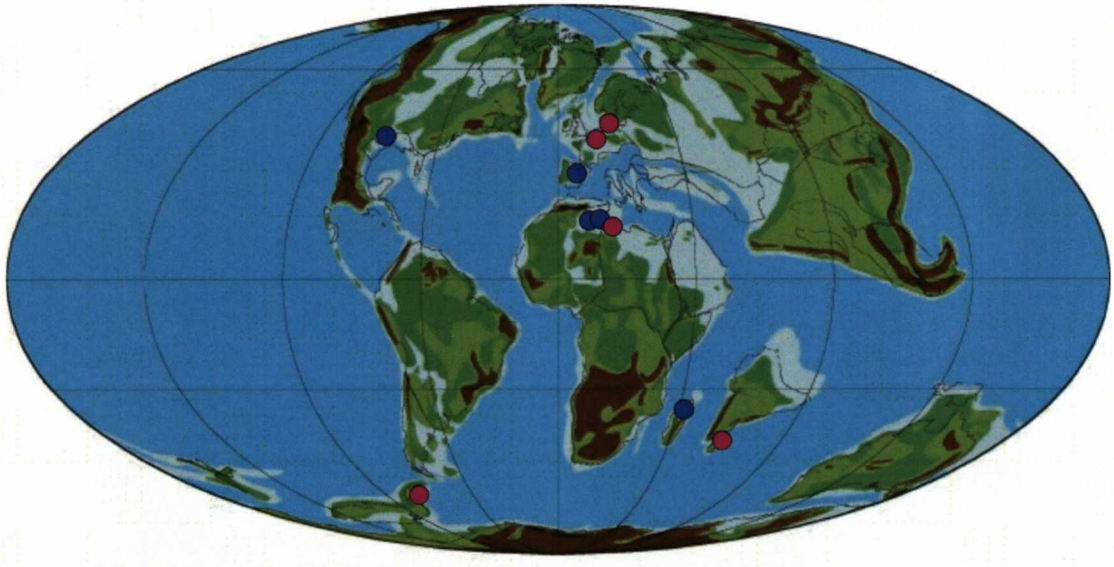

Figure 4.3: The location of the first occurrences of non-planktotrophic spatangoid (blue circles) and other echinoid (purple circles; data from Jeffery (1997)) clades plotted on Ziegler & Rowley's (1998) reconstruction of Maastrichtian palaeogeography.

4.4 DISCUSSION

4.4.1 Are the patterns observed real or artefact?

It is important to consider whether the patterns identified in this study represent real biological events or are, in fact, artefacts due to biases in factors such as sampling or the fossil record. This question is addressed here for both the temporal and spatial patterns that have been identified.

Temporal patterns

Palaeontological estimates of the ages of origination of clades are invariably underestimates because the first fossil occurrence is likely to occur some time after the origin of the clade (Benton & Ayala 2003). As a result, non-planktotrophic clades may have originated earlier than the times identified in this study. This has to be offset against the fact that the ranges for genera are likely to represent overestimates of their real stratigraphic range due to the limited stratigraphic resolution that is available for some taxa. For example, if the range of a genus is recorded in literature as "Campanian" it was assumed to span the entire stage, when in fact its range is likely to be shorter than this. As the fossil record of spatangoids is relatively complete it seems unlikely that these factors have a strong influence on the patterns observed. Analysis using the computer programme GHOSTS (Wills 1999) confirms this relative completeness: RCI (40.66), SCI (0.57) and GER (0.79) all indicate a relatively high congruence between tree topology and the stratigraphic record in comparison with other clades (e.g. Benton *et al.* 1999); there is also a significant variation from random stratigraphic data ($P = 0.01$).

It should be noted that the phylogeny can provide dates by which clades must have originated (assuming the phylogeny to be correct). This is because a clade must have diverged from its sister taxon by the first occurrence of the sister taxon in the fossil record. In the case of one of the

five switches to non-planktotrophy identified in this study, the *Diplodetus* clade, this would mean that the clade must have originated prior to the Campanian. However, the phylogenetic position of *Diplodetus* is not well resolved (indeed in the phylogeny of micrasterids presented in section 2.5 it lies in a position that does not require a range extension beyond the Campanian) and it is possible that the necessity of a pre-Campanian origin is an artefact of an incorrect phylogeny.

A further possibility that should be considered is that the first occurrence of multiple non-planktotrophic clades in the Campanian and Maastrichtian represents an improvement in the quality of the fossil record rather than the actual first occurrence of the clades. Although the question of whether the quality of the fossil record has varied significantly through the Phanerozoic remains contentious (e.g. Benton *et al.* 2000; Peters & Foote 2001; Smith 2001, 2007; Benton & Emerson 2007), marine diversity through geological time is known to be highly sensitive to variations in the volume of rock preserved (Smith & McGowan 2005, 2007). There are two non-exclusive hypotheses that could explain this observation (see Smith 2007 for review). Firstly, it could represent a biological phenomenon resulting from changes in speciation and extinction levels in response to changes in the area of shallow seas. Alternatively, it could represent a sampling artefact caused by the volume of rock available to scientists. If the second scenario is correct, then some patterns observed in the fossil record might result solely from biases in the rock record. However, this seems unlikely to be the case in this instance because, despite the fact that there is an apparent increase in spatangoid diversity at this time, rock volume falls through the Campanian and Maastrichtian as does overall marine diversity (see Smith 2001). This implies that this interval is, if anything, a period of decreasing preservation potential and so the near synchronous appearance of non-planktotrophic clades is unlikely to result from an increase in the quality of the fossil record, but rather from a real biological phenomenon. This conclusion is also

supported by the relative completeness of the spatangoid fossil record (see above).

Spatial patterns

It is known that taxonomic compilations tend to contain geographical bias because well-studied regions, such as Western Europe and North America, contribute more data than other regions (e.g. Jackson & Johnson 2001; Smith 2007). This translates to a latitudinal bias because the palaeogeographic location of these well-studied regions affects the relative contributions of data gathered from different latitudes (Allison & Briggs 1993). It is important to consider these biases when examining data on the spatial distribution of first occurrences of taxa (Jablonski *et al.* 2006). The approach to this problem taken by Jablonski *et al.* (2006) was to only use families that could be demonstrated to have good fossil records (those with ≥ 75% of Recent genera known as fossils) in their analysis of origination patterns in marine bivalves over the last 11 million years. Unfortunately, their approach is not applicable to the present study due to the greater age and smaller size of the study group.

In the Cretaceous, the vast majority of non-metamorphosed sedimentary rock in North America and Europe were deposited in temperate regions (Allison & Briggs 1993). The other main regions from which large numbers of Cretaceous echinoids have been collected and described include North Africa and Madagascar, which lay at sub-tropical and temperate latitudes respectively. Thus, while the data presented here and that presented by Jeffery (1997) provide no evidence for preferential origination of non-planktotrophic clades at high latitudes, it is hard to discount the possibility that the pattern is influenced by the fact that limited numbers of specimens that have been recovered from high palaeolatitudes. A more intensive collection effort in Antarctica or the southern parts of Australia and South

America might provide data to enable this issue to be addressed in the future.

4.4.2 What drives switches to non-planktotrophy?

In order to discover the factors that drove switches to non-planktotrophy it is important to understand the changes that these shifts in developmental strategy entail. Much is now known about the differences in developmental biology between planktotrophic and non-planktotrophic sea urchins. This is due largely to extensive work on the closely related sea urchins *Heliocidaris tuberculata*, which is planktotrophic, and *Heliocidaris erythrogramma*, which is lecithotrophic (reviewed in Raff 1996; Raff & Byrne 2006). From this work it is clear that switches from planktotrophic pluteus larvae to barrel-shaped lecithotrophic larvae involve major changes in early development. Important changes include:

- A 100-fold increase in egg content (Raff 1996).
- A major shift in the timing of the development of the large left coelom, which gives rise to much of the adult rudiment, from formation in advanced larvae (weeks after fertilization) to formation before the end of gastrulation (only hours after fertilization) (Ferkowicz & Raff 2001).
- A reallocation of blastomere fates so that a large proportion of blastomeres have adult fates and an associated change in cleavage pattern (Wray & Raff 1989, 1990).
- A change in the way the primary embryo axes are defined: all axes are defined maternally in *H. erythrogramma*, whereas the oral-aboral and left-right axes are defined later in development in *H. tuberculata* (Henry *et al.* 1990).
- A novel mechanism of gastrulation involving involution from the ventral side of the embryo (Wray & Raff 1991).

Progress has also been made in understanding the roles of regulatory genes in the evolution of the non-planktotrophic *H. erythrogramma* larva. Raff and his co-workers have produced a large body of work identifying the roles of various regulatory genes in the development of *H. erythrogramma*. The overall picture, summarized by Raff (1996), seems to be one of 'similar genes, different embryos'. In other words, the development of *H. erythrogramma* and *H. tuberculata* often involves the same regulatory genes, but because they are employed at different stages and in different regulatory environments the resulting larvae are very different. One particularly important insight was the work by Wilson *et al.* (2005a, 2005b) showing that the transcription factor *Gsc* is likely to have played an important role in the evolution of the non-planktotrophic *H. erythrogramma* larva.

Although the *differences* between planktotrophy and lecithotrophy are relatively well understood, the lack of a fossil record of echinoid larvae means that the evolutionary *transition* between the two strategies has remained poorly known. Smith *et al.* (2007) attempted to address this by studying the facultative planktotroph *Clypeaster rosaceus*, which represents an intermediate and presumably transitional form between obligate planktotrophy and non-planktotrophy. They found that *C. rosaceus* has early onset of a large left coelom, as seen in *H. erythrogramma* and other non-planktotrophs, while still maintaining the structures required for feeding; this shows that major developmental changes occur before the ability to feed is lost. While it had previously been assumed that developmental reorganisation occurred neutrally after the loss of feeding (Wray 1996), these findings suggest that the major developmental shifts are due to selection, perhaps for rapid metamorphosis, prior to the loss of feeding (Smith *et al.* 2007).

A further line of research that has led to insights into the transition from planktotrophy to non-planktotrophy in sea urchins is work on the hormonal

signalling systems that regulate metamorphosis (Heyland *et al.* 2004, 2005, 2006). Heyland *et al.* (2004) showed that the sand dollar *Leodia sexiesperforata*, an obligate planktotroph, completed metamorphosis in the absence of food when thyroid hormone was present. However, a second sand dollar, *Mellita tenuis*, an obligate planktotroph with smaller eggs than *L. sexiesperforata*, did not complete metamorphosis in the absence of food and the presence of thyroid hormone. These findings show that thyroid hormone can induce metamorphosis in obligate planktotrophs in the absence of food, but that the ability to do so depends on egg size. It had previously been shown that non-planktotrophic sea urchin larvae produce thyroid hormone endogenously but that the main source of thyroid hormone for planktotrophic sand dollars is ingested phytoplankton (Chino *et al.* 1994). Heyland *et al.* (2004, 2005) argue that these findings, coupled with their own results suggest that upregulation of endogenous thyroid hormone synthesis may be the proximate mechanism underlying the evolution of lecithotrophy in planktotrophic species with sufficiently large eggs. Further support for this hypothesis comes from the fact that the facultative planktotroph *Clypeaster rosaceus* fails to complete metamorphosis in the presence of the chemical goitrogen thiourea which blocks production of thyroid hormone, but that the addition of exogenous thyroid hormone reverses this effect (Heyland *et al.* 2006).

The changes that take place during switches to non-planktotrophy are used to inform the following discussion of the evolution of larval mode. While the present study identifies five shifts to non-planktotrophic development during the late Cretaceous, Peterson (2005) recognized that switches occurred in the opposite direction at least four, and perhaps as many as eight, times between the Late Cambrian and Middle Ordovician. Taken together, these studies show that switches in developmental mode (in either direction) are, at least in some circumstances, concentrated within particular intervals of geological history. This pattern of co-ordinated shifts in independent clades

strongly implies that extrinsic factors operating at the times of the shifts were responsible for driving these switches in developmental mode.

The two most likely external driving mechanisms are predation (Peterson 2005) and environmental change (e.g. Jeffery 1997). Having argued that the radiation of epifaunal suspension feeders in the Late Cambrian to Middle Ordovician was most probably responsible for the co-ordinated switches to planktotrophy that occurred at this time, Peterson (2005) argued that benthic predation was also likely to have driven later switches to non-plaktotrophy. The basis for this argument is that adaptations for non-planktotrophic development, such as large size and positive buoyancy, also serve to protect the larva from predation (though Vaughn & Strathmann (2008) found plutei cloned in response to predatory cues to produce smaller larvae, challenging the notion that bigger offspring are safer). In addition, it has been shown that reducing time to metamorphosis is advantageous in environments with high levels of predation (Wray 1995).

While predation may account for some of the selection pressure to evolve non-planktotrophy, it is unlikely to account fully for the co-ordinated switches to non-planktotrophic development that I have identified in sea urchins at the end of the Cretaceous. If benthic predation were responsible then we would expect to see a major radiation of benthic predators coinciding with the shifts. However, an examination of the relevant literature does not reveal evidence of such a radiation in the Campanian and Maastrichtian.

The other factor that has been suggested as a driving mechanism for switches to non-planktotrophy is environmental change. Foster (1974) suggested that cold temperatures might be responsible for the large number of brooding echinoids in the Eocene of southern Australia. However, it has subsequently been shown that there is no positive correlation between low palaeotemperature and high numbers of brooding taxa in this region

(McNamara 1994). As a result, it has been suggested that environmental instability is a more likely driver for switches to non-feeding or brooded development (McNamara 1994; Jeffery 1997). In the Campanian and Maastrichtian the climate was changing dramatically. Sea surface temperature was falling rapidly (e.g. Gale 2000) and, while total primary productivity was increasing (Faul *et al.* 2003), there is evidence that this was associated with increasing climatic seasonality (Steuber 1996; Francis & Poole 2002; Steuber *et al.* 2005; Dutton *et al.* 2007) and vigorous seasonal upwelling (Handoh *et al.* 2003). These changes would have led to the nutrient supply available to planktotrophic larvae becoming more abundant yet less reliable. Modern echinoderms living in areas with intermittent nutrient supply, such as strongly seasonal regions, tend to have either evolved so that their reproductive cycle coincides with the nutrient blooms, or else so that they develop with non-planktotrophic larvae and thus become independent of the nutrient supply (e.g. Pearse & Cameron 1991). The fact that the co-ordinated shifts in developmental mode that I have identified coincide with these major environmental changes, (but not with a marked change in predation - the other proposed driver) identifies environmental factors as the most plausible driving mechanism for the switches to non-planktotrophic development. Thus, it seems likely that there are intrinsic links between major developmental change and major environmental change.

The most likely scenario is that unreliable nutrient supply in the Campanian and Maastrichtian led to selection pressure for larger eggs. Eventually eggs would have reached sufficient size so as to remove the need to feed. Once this happened the developmental constraints associated with the requirement of producing a feeding larva would be removed. This would allow positive selection for rapid development prior to the loss of the ability to feed as observed in the sand dollar *Clypeaster roseaceus* by Smith *et al.* (2007). Studies on extant echinoids reveal that *Gsc* (Wilson *et al.* 2005a, 2005b) and thyroid hormone (Heyland *et al.* 2004, 2005, 2006) are likely to

have played an important role in this process. A reduced time to metamorphosis would be advantageous not only in terms of increasing survivorship in environments with low abundance of food, but also minimizing the risk of predation (Wray 1995).

It might be expected that other groups of marine invertebrates would also shift to non-planktotrophic development at the same time as the echinoids. While inference of larval mode it is possible in some other groups, such as gastropods (see Chapter 1) and bryozoans (e.g. McKinney & Taylor 1997), there has been little done in the way of surveying the timing of developmental shifts. However, cheilostome bryozoans appear to exhibit multiple shifts to brooded development from the Cenomanian onwards (Ostrovsky *et al.* 2006) and there is both direct (e.g. Blodgett *et al.* 2006) and indirect evidence (e.g. Valentine 1986; Valentine & Jablonski 1986) for non-planktotrophic invertebrates from the Mesozoic prior to the Campanian. More work is needed to understand the temporal, spatial and phylogenetic patterns in these groups.

4.5 SUMMARY

In conclusion, five independent shifts to non-planktotrophic development have been identified in Cretaceous spatangoids. The geographical distribution of the first occurrences of non-planktotrophic clades provides no support for the notion that they originate preferentially at high latitudes. However, it is difficult to discount the possibility that this pattern is a reflection of collection bias. Temporally, each of these non-planktotrophic clades made their first appearance in the fossil record in either the Campanian or Maastrichtian. This interval also contains the first known occurrences of non-planktotrophic development in four other echinoid orders (Jeffery 1997); no instances of non-planktotrophy in echinoids are known from any earlier than this. This pattern of co-ordinated switches does not seem likely to be an artefact of record or sampling biases and strongly

implies that extrinsic factors operation in the Campanian and Maastrichtian were responsible for driving switches to non-planktotrophic development. I suggest that environmental changes known to be operating during this interval are the most plausible driving mechanism.

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5. THE MACROEVOLUTIONARY CONSEQUENCES OF DEVELOPMENTAL STRATEGY IN CRETACEOUS SPATANGOIDS

5.1 INTRODUCTION

Theory predicts that many macroevolutionary, palaeoenvironmental and palaeobiogeographic factors will be intimately linked with developmental mode (see Jablonski & Lutz 1983 for review). For example, it is thought that because non-planktotrophs spend less time in the water column they will have lower dispersal potential. This is expected to result not only in narrower *geographical ranges*, but also in increased *speciation rates* (because it is more difficult for them to maintain gene flow between isolated populations), increased *extinction rates* (because they are more likely to be wiped out by local extinction events) and reduced *species longevity* (because of their greater extinction rate). It has also been suggested that larval mode may correlate with temperature (e.g. Foster 1974) and, as a result, to *latitude* (e.g. Thorson 1950), and *depth* (e.g. Thorson 1950). However, despite much discussion of these ideas in the literature, there have hitherto been remarkably few tests of them, especially for those factors involving geological timescales, which can only be studied using the fossil record (although see studies by Hansen 1978, 1980; Jablonski 1982, 1986; Jeffery & Emlet 2003). Furthermore, with the exception of Jeffery & Emlet (2003), those palaeontological studies that have been carried out have lacked phylogenetic constraint. This chapter aims to address this by assessing how these factors correlate with developmental mode in Cretaceous spatangoid echinoids. Echinoids are unusual because larval modes can be determined from an inspection of the fossilized adult test, and in spatangoids the apical system is more readily preserved than in some other sea urchin groups. In order to assess whether correlation between these factors and larval mode exists, data on each of these factors have been gathered from the literature and are compared with a dataset of larval modes inferred from fossil taxa.

It is important that evolutionary history is considered when carrying out comparative analyses such as these because it is possible that sister species share similar traits, such as geographical range (see Jablonski & Hunt 2006 for discussion of the heritability of this trait), as a result of their shared evolutionary history. Treating species as independent data points may therefore be flawed and lead to spurious correlations.

Two approaches were taken here. Firstly I analyzed raw data to assess whether any correlation exists between larval mode and the traits of interest. This first approach assumes that these traits evolve rapidly and independently. Secondly phylogenetic comparative methods (e.g. Harvey & Pagel 1991) were used. These methods do not treat species as independent data points and aim to take shared ancestry into account. The approach used here was *independent contrasts* (Felsenstein 1985) because it is the most commonly applied method, allowing comparison with many other studies, and because it can be readily implemented using the computer programme CAIC (Purvis & Rambaut 1995). This method makes phylogenetically independent comparisons between pairs of taxa.

5.2 MATERIALS AND METHODS

5.2.1 Phylogenetic analysis

The phylogenetic analysis used here utilizes the same characters and character states as the genus level analysis presented in Section 3.3. However, the taxonomic coverage is somewhat different to that of the earlier analysis. The present analysis is carried out at the species level and includes species listed in Chapter 2 as being valid. I exclude: (a) species for which developmental mode is unknown; and (b) species in genera with poorly known taxonomy (i.e. the toxasterids, *Micraster*, *Gibbaster*, *Hemiaster*, *Mecaster* and *Bolbaster*) because few of the large numbers of

species that have been described are likely to represent real biological entities and so their inclusion could lead to spurious results.

Following the exclusion of the species discussed above, the dataset comprised 30 species in 22 genera (of 37 genera recognized in this thesis). Inclusion of only species with known larval mode might potentially lead to some bias, as those excluded tend to be rare species that I have not been able to examine in this thesis and, as a result, they could perhaps have lower than average species durations and geographical ranges. The exclusion of taxa whose taxonomy is poorly known could also introduce a bias as the excluded genera tend to be those with very large numbers of described species and, at first sight, might seem to be portions of the tree with unusually high speciation rates and short species ranges. However, as many of these species are likely not to be valid their inclusion cannot be justified. One potential solution might be to include the species groups proposed in Chapter 2 of this thesis in the analyses. However, I have elected not to take this approach: I do not consider these groups to be equivalent to the other species in the analysis, so including them would not be meaningful.

The data matrix is presented in Table 5.1. The analytical methodology is identical to that used in the genus level phylogenetic analysis of Section 3.3.

Toxaster	0001110011	?121100102	1103110000	2000000000	00010
Iraniaster affinidouvillei	0021110001	0102201100	10021-0110	1100001000	00010
Iraniaster douvillei	0021110001	0102201100	10021-0110	1100001000	00010
Iraniaster morgani	0021110001	0102201100	10021-0110	1100001000	00010
Palhemiaster peroni	0021110000	0102101201	1002?100?0	1010011010	00010
Palhemiaster calvini	0021110000	0102101201	1002?100?0	1010011010	00010
Holcopneustes cristatus	1031110002	0100201200	100??020?0	?0?1??1001	00010
Periaster elatus	00(12)1110001	0102101201	1001102001	0001011110	01010
Abatus pseudoviviparus	2331100001	0122101201	1100102000	0001011110	01010
Linthia payeni	0031110001	0102101201	1001002001	0011011110	01010
Linthia sudanensis	0031110001	0102101201	1001002001	0011011110	01010
Schizaster variabilis	003111?001	1102101201	1001002000	0001011110	01010
Holanthus hawkinsi	0011000001	0100101211	1011(01)02000	1000001010	00010
Gregoryaster jacobi	0031110001	1100001201	1002110000	1001101000	00010
Leiostomaster sp.	0021001000	0102001201	101??120?0	?010101O?0	00010
Leymeriaster leymeriei	0021001002	1100101201	100??110?0	?001111010	00010
Leymeriaster similis	0021001002	1100101201	100??110?0	?001111010	00010
Leymeriaster nucleus	0021001002	1100101201	100??110?0	?001111010	00010
Proraster morgani	2022211001	1121111211	1001002000	1001011000	00010
Mauritanaster mirabilis	103111?000	2110101201	200??020?1	?0010?10?0	??010
Heterolampas maresi	0021010011	2110101201	2003302000	1000011000	00010
Plesiaster peini	00111?0001	0102101101	1101010000	1011000- - -	10110
Diplodetus americanus	0011110002	0100101100	0?01002000	1002100- - -	10110
Isaster aquitanicus	011000100?	0100100100	0001(01)02000	2000100- - -	10100
Cyclaster integer	0111111001	0100101100	0001102001	1102001010	10110
Ovulaster auberti	101111?00?	?110000002	?102002001	20?1000- - -	10110
Homoeaster auberti	1011110001	0112100002	2001002000	2011001001	00010
Homoeaster tunetanus	1011110001	0112100002	2001002000	2011001001	00010
Coraster beneharnicus	102001?001	?010000002	?101402021	200200101 -	00010
Cottreaucorys blayaci	101001?001	?010000002	??01402001	200100101 -	00020

Table 5.1: Data matrix used in the phylogenetic analysis.

5.2.2 Species data

The following data were collected for each of the species included in the analyses. The data are presented in Tables 5.2 (for continuous variables) and 5.3 (for depth, which was treated as a categorical variable).

Developmental mode

Developmental modes were inferred using crystallographic and morphological criteria. The methodology is discussed in detail in the preceding chapter.

Species longevity

The durations of species were calculated by summing the durations of the stages in which they are known to occur. This approach tends to over-estimate the duration of a species; this is because a species reported in the literature as, for example, "Campanian" is assumed to span the whole stage, when this may not actually be the case. The fact that the stages are not of uniform duration could potentially lead to different sizes of error in taxa that occur in different stages (Jeffery & Emlet 2003). The full ranges of species that extend into the Palaeocene are given (no species have ranges that extend down into the Jurassic).

Geographical range

A number of metrics exist to estimate geographical ranges of species (e.g. Emlet 1995; Gaston 1994). In order to calculate the geographical range, records of species occurrence localities from the literature and from museum collections were first plotted onto the palaeogeographical reconstruction of Blakey (http://www2.nau.edu/rcb7/globaltext2.html) closest to the age from which the species is known. The geographical range of each of the species was measured as: (1) the maximum number of degrees longitude; (2) the maximum number of degrees latitude; and (3) the longest straight-line distance in kilometres between specimens recovered from age-equivalent

strata. This approach minimizes the possibility that ranges are artificially inflated in species that have migrated through time (Jeffery & Emlet 2003). The longest straight-line distance was calculated using spherical geometry. When calculating these metrics, and subsequent metrics, species known from a single locality were assigned a range of 1° or 1 km. Decimal degrees are used throughout this chapter.

Latitude

Palaeolatitudes of fossil localities were plotted onto palaeogeographical reconstructions as described above. The palaeolatitude of a species was recorded as: (1) the midpoint between its most northerly and most southerly occurrences; and (2) the maximum latitude from which it has been recorded.

While the approach of measuring latitude as the midpoint of the latitudinal range of a species has been widely applied in the literature (e.g. Long *et al.* 2007), it seems to have important limitations, particularly where species span the equator. A hypothetical species found at the north and south poles would be recorded at the equator using this method. Nevertheless, this method is retained in order that the results can be compared to those of other studies. One alternative would be to measure the mean of the highest and lowest latitudes from which it is known, regardless of hemisphere. However, because only one species in the present dataset spans the equator, and the results of such a study would be practically identical, this approach is not applied here.

Depth

The depth at which species lived was inferred from independent sedimentological studies in the literature. This was recorded as a categorical variable with three categories, which correspond to those of Smith & Jeffery (1998): shallow (within fair-weather wave base); intermediate (within storm wave base); and deep (basinal muds and chalks). I examined:

(1) maximum depth; (2) minimum depth; and (3) number of depth zones occupied.

5.2.3 Comparative analyses

In order to assess the relationships between developmental mode and the various species level traits, two types of analysis were carried out. The first approach tested whether planktotrophic and non-planktotrophic species had significantly different geographical ranges, species longevities, palaeolatitudes and depths to one another. For the continuous variables these tests were carried out using a Mann-Whitney *U*-test (as the data were non-parametric) to test the null hypothesis that there is no difference between planktotrophic and non-planktotrophic species for each trait. As depth was treated as a categorical variable the chi-squared test is the appropriate test in this case. This tests the null hypothesis that there is no association between larval mode and depth.

The Mann-Whitney *U*-test assumes that each species can be treated as an independent data point. However, closely related species may share traits simply as a result of their shared ancestry and, if this is the case, then the assumption that the species represent independent data points cannot be justified (e.g. Harvey & Pagel 1991). It is possible that the species level traits of interest here are heritable (e.g. geographical range Jablonski 1987, 2007; Jablonski & Hunt 2006) and are thus liable to be influenced by shared phylogenetic history. As a result, the second analyses used phylogenetic comparative analyses (Felsenstein 1985) to control for the effects of shared ancestry. CAIC (Purvis & Rambaut 1995) was used to implement the *independent contrasts* method, which makes phylogenetically independent comparisons between pairs of taxa. Branch lengths were assumed to be equal across the tree. In order to be sure that the assumptions used in the statistical analyses are violated, prior to further analysis I confirmed that: (1) the contrasts in the explanatory variable were plotted against the standard

deviation of contrasts in order to ensure the heterogeneity of the contrasts generated (Garland *et al.* 1992); and (2) there was no significant correlation between the contrasts and their standard deviations (Purvis & Rambaut 1995). A one-sample *t*-test against a mean of zero was used to test the significance of the standardized contrasts (Purvis & Rambaut 1995).

5.2.4 Speciation rates

Analysis of speciation rates using only the species included in the comparative analyses is clearly flawed. This is because large numbers of species are missing. Instead speciation rates were estimated using occurrence data for all species assigned to genera with well-understood taxonomy and using the genus-level phylogeny presented Section 3.3, with poorly known taxa excluded. I made the assumption that species with unknown developmental mode had the same mode as their congeners with known developmental strategy. While no examples have been identified where this assumption is violated in Cretaceous spatangoids, it is known to be broken occasionally such as in the extant camarodont genus *Heliocidaris* (where, of the two extant species, *H. tuberculata* is planktotrophic and *H. erythrogramma* is non-planktotrophic). As switches from planktotrophy to non-planktotrophy are thought to be considerably more likely than switches in the opposite direction (e.g. Strathmann 1978), any violation of the assumption that congeners share the same developmental mode would most likely be due to unidentified switches to non-planktotrophy. Such unidentified switches would result in genera listed as planktotrophic including some non-planktotrophic species and might lead to the underestimation of any differences between planktotrophs and non-planktotrophs.

The dataset was analysed in three different ways. Firstly the method of Jablonski (1986) was used to measure speciation rate in each genus. This measures the number of speciation events per species per million years (i.e. number of species/sum of species durations). Secondly the same data were

analysed using comparative phylogenetic methods (discussed above). The dataset was analysed in CAIC in the same way as described above using the genus level phylogeny of Section 3.3 after it had been pruned to remove poorly known genera. The third method was to compare the proportion of speciation events involving ancestors of a given larval mode to the proportion of species in the group with that larval mode (Hart *et al.* 1997; Jeffery & Emlet 2003). The dataset used in these analyses is presented in Table 5.4.

Genus	Species	Species longevity (m.y.)	Longitude range (degrees)	Latitude range (degrees)	Straight-line (km)	Latitude midpoint (degrees)	Maximum latitude (degrees)	Larval mode
Abatus	*pseudoviviparus*	10	1	1	1	30	30	N
Coraster	*beneharnicus*	10	16	10	1630	39.5	42	P
Cottreaucorys	*blayaci*	23	7.5	7	3761	28.5	32	P
Cyclaster	*integer*	10	53	10	4995	32	38	N
Diplodetus	*americanus*	7	10	5	1510	32.5	32.5	N
Gregoryaster	*jacobi*	21	20	15	8576	37.5	45	P
Heterolampas	*maresi*	11	1	1	1	25	25	N
Holanthus	*hawkinsi*	10	90	12	1606	36	42	P
Holcopneustes	*cristatus*	10	20	1	1922	30	30	P
Homoeaster	*auberti*	1	9	1	909	25.5	26	P
Homoeaster	*tunetanus*	26	45.5	8	4153	36	40	P
Iraniaster	*affinidouvillei*	11	10	5	1218	12	15	P
Iraniaster	*douvillei*	22	5	16	2247	10	18	P
Iraniaster	*morgani*	18	1	1	1	10	10	P
Isaster	*aquitanicus*	19	3.5	6	739	35	38	P
Leiostomaster	sp.	11	13	32	3824	9	25	N
Leymeriaster	*leymeriei*	13	2	2	241	34	35	P
Leymeriaster	*nucleus*	9	6	11	1276	42.5	48	P
Leymeriaster	*similis*	4	2	8	893	37	37	P
Linthia	*payeni*	18	22	21	3266	19.5	30	P
Linthia	*sudanensis*	15	1	1	1	13	13	P
Mauritanaster	*mirabilis*	7	2	1	190	31	31	N
Ovulaster	*auberti*	22	9	1	909	25.5	26	P
Palhemiaster	*calvini*	12	13	6	1247	25	28	P
Palhemiaster	*peroni*	17	7	2	798	10	11	P
Periaster	*elatus*	4	2	1	173	39	39	P
Plesiaster	*peini*	15	3.5	1	374	27	27	P
Proraster	*morgani*	21	4	10	610	23	28	P
Schizaster	*variabilis*	14	22	4	2104	32	34	P

Table 5.2: Continuous data used in the analyses in this chapter; see text for full details. (P = planktotrophy; N = non-planktotrophy)

Genus	Species	Maximum depth	Minimum depth	Depth zones	Larval mode
Abatus	*pseudoviviparus*	Deep	Deep	1	N
Coraster	*beneharnicus*	Deep	Deep	1	P
Cottreaucorys	*blayaci*	Deep	Deep	1	P
Diplodetus	*americanus*	Deep	Intermediate	2	N
Gregoryaster	*jacobi*	Deep	Deep	1	P
Iraniaster	*affinidouvillei*	Intermediate	Intermediate	1	P
Iraniaster	*douvillei*	Intermediate	Intermediate	1	P
Iraniaster	*morgani*	Intermediate	Intermediate	1	P
Isaster	*aquitanicus*	Deep	Intermediate	2	P
Leiostomaster	sp.	Deep	Deep	1	N
Leymeriaster	*similis*	Intermediate	Intermediate	1	P
Linthia	*payeni*	Shallow	Shallow	1	P
Linthia	*sudanensis*	Shallow	Shallow	1	P
Mauritanaster	*mirabilis*	Deep	Intermediate	2	N
Palhemiaster	*calvini*	Intermediate	Shallow	2	P
Periaster	*elatus*	Shallow	Shallow	1	P
Plesiaster	*peini*	Deep	Deep	1	P
Schizaster	*variabilis*	Intermediate	Shallow	2	P

Table 5.3: Data used in chi-squares tests for association between depth and larval mode. See text for details.

Genus	Number of speciations	Sum of ranges	Speciation rate	Larval mode
Iraniaster	6	80	0.075	P
Palhemiaster	4	46	0.087	P
Lambertiaster	1	21	0.047	P
Holcopneustes	2	20	0.100	P
Periaster	3	9	0.333	P
Abatus	1	10	0.100	N
Linthia	3	43	0.070	P
Schizaster	5	60	0.083	P
Holanthus	1	10	0.100	P
Leiostomaster	1	11	0.091	N
Leymeriaster	8	75.5	0.106	P
Proraster	5	81	0.062	P
Mauritanaster	1	7	0.143	N
Heterolampas	1	11	0.091	N
Plesiaster	4	47	0.085	P
Diplodetus	7	50	0.140	N
Isaster	1	19	0.053	P
Cyclaster	7	45.8	0.153	N
Ovulaster	3	49	0.061	P
Homoeaster	4	44	0.091	P
Orthaster	1	18	0.056	P
Cottreaucorys	2	30	0.067	P
Coraster	2	20	0.100	P

Table 5.4: Table showing the number of speciation events within each genus, the sum of the stratigraphic ranges of the species in the genus, the speciation rate of the genus per species per million years (i.e. number of speciation events/sum of species ranges), and the larval mode of the genus (P = planktotrophic; N = non-planktotrophic).

5.3 RESULTS AND DISCUSSION

5.3.1 Phylogenetic analysis

The tree produced by the phylogenetic analysis that forms the basis of the subsequent phylogenetic comparative analyses is presented in Figure 5.1.

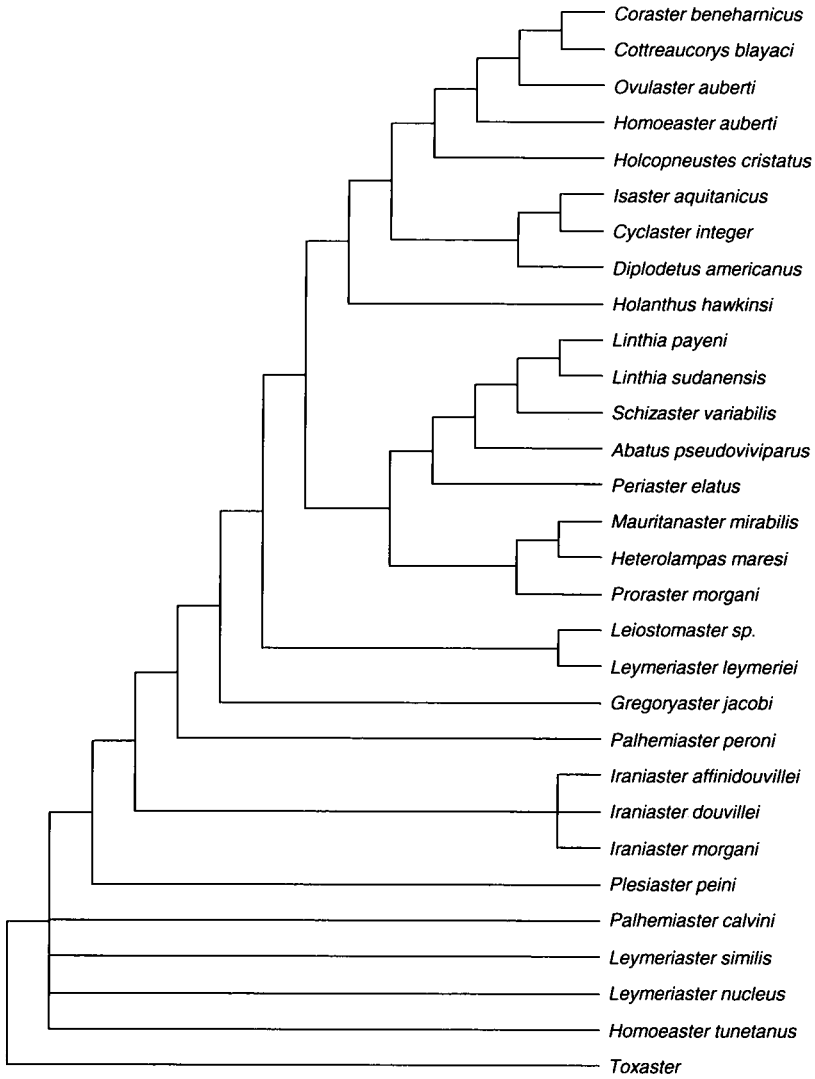

Figure 5.1: The tree produced by the phylogenetic analysis that is used as the basis for the phylogenetic comparative analyses in this chapter. See text for details of analytical methods.

5.3.2 Developmental strategy and stratigraphic range

The mean stratigraphic range for planktotrophic species included in this analysis is 14.57 million years (N = 23; SD = 6.63) compared to 9.33 million years (N = 6; SD = 1.86) for non-planktotrophic taxa. A Mann-Whitney *U*-test shows that this difference is significant ($P = 0.047$). However, when phylogeny was taken into consideration the difference was found not to be significant ($P = 0.213$), meaning it is not possible to discount the possibility the association between larval mode and species range is due to shared ancestry.

A number of previous studies have found that stratigraphic ranges are shorter in species with non-planktotrophic larvae than they are in species with planktotrophic larvae (Hansen 1978, 1980; Jablonski 1982, 1986; Gili & Martinell 1994). These findings also match the expectations of theoretical models (Shuto 1974; Scheltema 1977; Jablonski & Lutz 1983), which predict that species that lack the ability to disperse long distances will have restricted geographical and ecological ranges and so will be more likely to be wiped out by a local catastrophe. This is expected to result in higher extinction rates and shorter stratigraphic ranges than planktotrophic species. However, these studies do not take the phylogeny of the groups in question into consideration. When Jeffery & Emlet (2003) carried out a comparative phylogenetic analysis on the temnopleurid echinoids, they also found that while conventional statistics suggested that there was a significant difference between the species ranges of planktotrophs and non-planktotrophs, independent contrasts did not give a significant result. Jeffery & Emlet (2003) noted that, as in the present study, CAIC never reported a significant association between developmental mode and any species level trait. They suggest that one possibility is that the small number of independent contrasts in their analysis and consequent lack of power of the tests could be responsible. Though there are a slightly higher number of independent contrasts in the present analysis (5 compared to 3 in Jeffery & Emlet (2003)),

this could be a factor here too. However, when the Tertiary temnopleurid data of Jeffery & Emlet and the data on Cretaceous spatangoids used in this chapter were combined into a single dataset, CAIC still did not give a significant result ($P = 0.120$) even though there were now eight phylogenetically independent contrasts.

5.3.3 Developmental strategy and geographical range

The analyses showed that there is only a small difference in mean geographical range between planktotrophic species and non-planktotrophic species. When longitudinal range is used, planktotrophic species have a higher mean range (13.96°; N = 23; SD = 19.5) than non-planktotrophic taxa (13.33°; N = 6; SD = 20.09). The Mann-Whitney *U*-test confirms that this difference is not statistically significant ($P = 0.546$). When latitudinal range or straight-line distance is used non-planktotrophic species have a slightly larger mean range (latitudinal range: 8.33°; N = 6; SD = 12.13; straight-line distance: 1753.5 km; N = 6; SD = 2165.2) than planktotrophs (latitudinal range: 6.52°; N = 23; SD = 5.70; straight-line distance: 1680.6 km; N = 23; SD = 1882.3), though again a Mann-Whitney *U*-test confirms that this difference is not statistically significant (latitudinal range: $P = 0.694$; straight-line distance: $P = 0.733$). Comparative phylogenetic methods also find that that there is no significant difference between the geographical ranges of planktrophic and non-planktotrophic species regardless of whether longitudinal range ($P = 0.736$), latitudinal range ($P = 0.278$), or straight-line distance ($P = 0.320$) is measured.

The finding here that there is no association between planktotrophy and larger geographical ranges is highly surprising. Theory predicts that species with planktotrophic larvae that can spend long periods in the water column will disperse over greater distances and because the larval stage of benthic marine organisms offers the main opportunity for dispersal, this is expected to lead to greater geographical ranges in planktotrophic species (Shuto

1974; Scheltema 1977; Jablonski & Lutz 1983). This theoretical prediction is borne out in a number of previous analyses on both fossil (Hansen 1978, 1980; Jablonski 1982, 1986, 1987; Jeffery & Emlet 2003; Jablonski & Hunt 2006) and Recent (Emlet 1995) groups. As the results contradict several previous studies that have found a significant relationship between larval mode and geographical range, it seems likely that they reflect some bias in sampling.

One important difference between this analysis and the previous work that did find a significant correlation between non-planktotrophy and narrower geographical ranges is that the previous studies were restricted to particular geographical regions (Gulf Coast, USA: Hansen 1978, 1980; Jablonski 1982, 1986; southern Australia: Jeffery & Emlet 2003). It is possible that carrying out analyses of geographical range on a global scale may be problematic. Other global studies have failed to find expected relationships between geographical range and other factors. For example, Smith & Jeffery's (1998) global study was unable to find a correlation between geographical range and survivorship across the Cretaceous-Tertiary boundary, while regionally based work (and global studies of other groups) has suggested that such a correlation does exist (e.g. Jablonkski & Raup 1995).

The reason for these possible problems may be due to different collection and recording biases operating in different regions of the world. Within a region collection is likely to be reasonably even with occurrence data recorded with broadly equivalent accuracy, so any biases in the data are likely to apply equally across the entire dataset. However, between regions collection and recording biases are likely to change considerably. This could result in geographical range data not being comparable between regions and, if so, it may not be meaningful to combine the data into a global level datasets. For example, in the data used in these analyses there is a significant difference between the geographical range (measured here as the

longest straight-line distance) species from North America (mean = 1620km; N = 3 (1 non-planktotroph); SD = 439.02) and those from North Africa (mean = 530km; N = 6 (2 non-planktotrophs); SD = 394.69) ($P = 0.024$). As there is no obvious biological explanation, this could be due simply to collection biases. This area requires further work on larger datasets, but this finding suggests that caution is required in the interpretation of global datasets of geographical range.

5.3.4 Developmental mode and latitude

The mean of the midpoints of the latitudinal ranges of planktotrophic species was 27.28° (N = 23; SD = 10.51) compared to 26.58° (N = 6; SD = 9.02) for non-planktotrophic species. While this would suggests that planktotrophic taxa occur at marginally higher latitudes than non-planktotrophs a Mann-Whitney *U*-test reveals that this difference is not significant ($P = 0.655$). On the other hand, if the maximum latitude at which a species is recorded is considered, rather than the midpoint of its latitudinal range, then non-planktotrophs have a higher mean (32.25°; N = 6; SD = 4.91) than planktotrophic species (30.17°; N = 23; SD = 10.96). However, once again a Mann-Whitney *U*-test suggests that this difference in not significant ($P = 0.733$). Comparative phylogenetic analysis also shows that these differences are not significant ($P = 0.307$ for midpoint of latitudinal range; $P = 0.300$ for maximum latitude).

These findings, and the fact that no trend for preferential origin of non-planktotrophic clades in high latitudes could be identified by either Jeffery (1997) or in this thesis (Chapter 4), would seem to be at odds with findings from Recent echinoids. These show that there is a significant correlation between decreasing planktotrophy and increasing latitude (Emlet *et al.* 1987; Emlet 1990). In addition, brooding (Philip & Foster 1971) and planktonic non-planktotrophy (Pearse *et al.* 1991; Pearse 1994) are both unusually abundant in Antarctic waters. However, it seems that this abundance is

predominantly an Antarctic, rather than polar, phenomenon (Philip & Foster 1971; Pearse *et al.* 1991). In addition, the modern Antarctic echinoid fauna is actually dominated by planktotrophs, when considered in terms of individuals rather than species, suggesting that feeding larvae are advantageous in modern Antarctic waters (Poulin *et al.* 2002). These facts suggest that the abundance in Antarctic waters of brooding, and perhaps non-planktotrophy in general, is likely to be due to species selection that occurred in the region in the past, rather than selection for current conditions (Poulin *et al.* 2002). While it should be noted that no Cretaceous Antarctic species were included in the present analysis, the findings, as well as those from previous work, suggest that latitude may not play an important role in determining the predominant larval mode.

5.3.5 Developmental mode and depth

I was only able to collect depth data for a subset of the species studied in the analyses in this chapter. As a result the comparative analyses of depth include 18 species, of which 14 are planktotrophic and four are non-planktotrophic. Chi-squared tests revealed no significant association between larval mode and maximum depth ($P = 0.076$), minimum depth ($P = 0.364$) or the number of depth zones occupied ($P = 0.423$). Analysis in CAIC was not carried out as the *independant contrasts* method requires continuous, rather than categorical data (Purvis & Rambaut 1995).

These results should be treated with caution due to the reduced sample size and the fact that work on Recent echinoids, in which depth can be ascertained with considerably greater accuracy, has reported a significant correlation (Emlet *et al.* 1987). The analyses of depth presented here have been hampered by considerable difficulties in obtaining depth data for some species. This is particularly true for species from North Africa and results from poor documentation of the locations and lithologies of specimens in museum collections and the literature. For example, the type material of

Heterolampas maresi is recorded as being from "Kef Matrek, Algeria" with no lithological information. However, an Internet search for Kef Matrek reveals no further information that would allow the locality to be linked to information on the depositional environment. These problems emphasise the importance of good documentation of occurrence data in museum collections and in papers that record fossil finds. It is also vital that when such information exists it is conserved when, for example, museum labels begin to age and become difficult to read. New collections that record the pertinent information may allow questions such as the relationships between depth and other factors to be answered with greater confidence in the future.

5.3.6 Developmental mode and speciation rate

When speciation rate is measured per species per million years (Jablonski 1986) a Mann-Whitney *U*-test allowed the null hypothesis that there is no significant difference between the speciation rates of planktotrophic and non-planktotrophic species to be rejected ($P = 0.045$). This accords with several studies that have suggested that non-planktotrophic taxa have higher rates of speciation than non-planktotrophs (Hansen 1978, 1980, 1982, 1983; Jablonski & Lutz 1983; Jablonski 1986; Jeffery & Emlet 2003).

When applied to extinct groups, Jablonski's (1986) method of measuring speciation rate (number of speciation events/sum of species durations) will always give the same result as that for extinction rate (number of extinction events/sum of species durations). The number produced in fact represents the mean of the species durations within the group, which is likely to result from the interaction of both speciation and extinction rates, both of which may vary through time. Thus, it seems that the metric is related to speciation rate, but does not measure it directly.

As Jeffery & Emlet (2003) have pointed out, analyses such as this one do not explicitly take phylogeny into account. Two methods of analysis were

used to assess whether there was a difference between the speciation rates of planktotrophic and non-planktotrophic species when phylogeny was considered. The first of these utilized comparative phylogenetic methods and suggested that there is no significant difference ($P = 0.781$).

In the second analysis it was shown that planktotrophic ancestors were involved in 60 out of 73 (82.19%) speciation events. This represents a higher percentage than that of planktotrophic species in the Cretaceous spatangoid fauna, where they make up 56 out of 75 (75.68%) of the total number of species. Similar patterns have been observed in other groups of echinoderms. Hart *et al.* (1997) found that in asterinid starfish 6 out of 11 (54.5%) speciation events occurred in an ancestor with planktotrophic larvae when feeding larvae only accounted for 3 out of 12 (25%) of asterinid species. Similarly, Jeffery & Emlet (2003) found that in temnopleurid echinoids more speciation events involved planktotrophic ancestors (9 out of 15; 60%) than non-planktotrophic ancestors (6 out of 15; 40%) despite the fact that there were more non-planktotrophic species (9 out of 16; 56.25%) than planktotrophic (7 out of 16; 43.75%). At first sight these findings would seem to contradict those of the analysis using the method of Jablonski (1986) and suggest that planktotrophic ancestors are the more likely to speciate. However, when planktotrophy lies basally and non-planktotrophy lies near the tips of the branches then this is likely to artificially inflate the speciation rate of planktotrophs when it is measured in this way. In asterinid starfish the finding relies heavily on the assumption of Hart *et al.* (1997) that switches are unidirectional (from planktotrophy to non-planktotrophy) and irreversible. For example, if it were assumed that switches are equally likely in either direction (the reality probably lies somewhere between these two extreme assumptions) then only 1 out of 11 (9.1%) speciation events would involve a planktotrophic ancestor. In the Cretaceous spatangoids we know from analysis of the stratigraphic occurrence of species with planktotrophic and non-planktotrophic larvae (previous chapter) as well as from the

phylogeny of the group that non-planktotrophy evolved only relatively late in the evolutionary history of the Cretaceous spatangoids. Thus, while the ratio of speciation events with a planktotrophic ancestor is higher than the proportion of planktotrophs in the fauna, it seems likely that this is the result of branching events at internal nodes in the tree prior to the evolution of non-planktotrophy.

Like the method of Jablonski (1986), the method of Hart *et al.* (1997) is not a direct measure of speciation rate. It counts the ratio of speciation events with planktotrophic ancestors and compares this to the proportion of planktotrophs in the clade. It is not a measure of speciation rate as it contains no element of time. Furthermore, as we have seen, it is likely to give inflated values to the developmental mode that lies in the basal portions of the tree.

Two hypotheses have been presented to account for increasing numbers of planktotrophic species in clades through time. Firstly, under species selection (Hansen 1978, 1982; Jablonski & Lutz 1983; Jablonski 1986) the increase is due to non-planktotrophic species increasing in number because they are more likely to speciate. Alternatively, in species sorting due to developmental shifts (Duda & Palumbi 1999; Hart 2000) non-planktotrophic species proliferate simply because switches from planktotrophy to non-planktotrophy are considerably more likely than shifts in the opposite direction. Duda & Palumbi (1999) identify predictions made by each hypothesis that might be used to distinguish between them: species selection will produce speciose monophyletic clades of non-planktotrophic species, whereas species sorting due to developmental shifts will result in many small independent non-planktotrophic clades.

This analysis finds evidence for species selection in the form of switches to non-planktotrophy that are followed by multiple speciation events leading to

relatively large monophyletic clades of non-planktotrophic taxa (e.g. *Cyclaster*, *Diplodetus*). Furthermore, analysis showed that these clades have significantly higher speciation rates than planktotrophic clades. On the other hand, there is also evidence of species sorting due to developmental shifts in that there are examples of switches to non-planktotrophy that are followed by zero or one speciation event(s) (*Mauritanaster*, *Heterolampas*, *Leiostomaster*). Thus this study suggests that a combination of species selection and species sorting due to developmental shifts is in operation in the Cretaceous spatangoids.

5.4 SUMMARY

To summarize, analysis of raw data showed that there is a significant association between non-planktotrophic larval development and both increased speciation rates and reduced species longevity. On the other hand, no significant associations were identified between larval mode and geographical range, latitude or depth. When phylogeny was taken into consideration it was not possible to discount the possibility that significant relationships result simply from shared ancestry. The analyses found support for the operation a combination of both species selection and species sorting due to developmental shifts within the Cretaceous spatangoids. Future studies with larger datasets and better-constrained locality and depth information are needed to confirm whether there is really no correlation between larval mode and geographical range, latitude and depth.

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6. CONCLUSIONS

- Non-planktotrophic development arose in five independent clades of Cretaceous spatangoids.

- Each of the five non-planktotrophic clades originated in the Campanian or Maastrichtian, with no examples of non-planktotrophy known from before this interval.

- The co-ordinated pattern of shifts that was found suggests that extrinsic factors operating at this time were responsible for driving the shifts; I suggest that environmental change is the most plausible factor.

- No support was found for the hypothesis that non-planktotrophic clades originate preferentially at high latitude, despite their abundance at high latitudes in modern oceans.

- Significant associations were identified between non-planktotrophic development and shorter species durations and increased speciation rates. Phylogenetic comparative methodology was unable to rule out the possibility that these associations are simply due to shared ancestry.

- No significant association could be identified between larval mode and geographic range, latitude or depth.

7. SUGGESTIONS FOR FUTURE WORK

- In spite of the work in this thesis, the taxonomy and phylogeny of some portions of the spatangoid tree are still in need of revision. In particular the toxasterids, which were excluded from this thesis due to time constraints, are in need of taxonomic revision. The systematics of the genera *Micraster*, *Gibbaster*, *Hemiaster*, *Bolbaster* and *Mecaster*, each of which contains large numbers of nominal species, also requires further work. Detailed morphometric analyses are needed in order to establish the validity of the large numbers of nominal species in these genera.

- Our understanding of higher-level spatangoid phylogeny could be improved by molecular phylogenetic analyses with increased taxon sampling. In particular, the most comprehensive analyses to date could be extended by including extant representatives of the Hemiasteridae (e.g. *Kupeia*, *Leiostomaster*, *Holanthus*, *Palaeostoma* or *Sarsiaster*), Aeropsidae (*Aeropsis*) and Micrasteridae (e.g. *Cyclaster*).

- The approach of studying the timing and location of origination of non-planktotrophic clades, as used in this thesis, has not been widely applied to other groups. There is potential for such studies in other marine invertebrate taxa such as molluscs, brachiopods and bryozoans. Surveys of larval mode in these taxa have the potential to identify patterns in the timing and location of shifts between the two major developmental modes. They could also determine whether any such patterns, are taxonomically widepread. For example, they could determine whether the co-ordinated shifts observed in Cretaceous echinoids are observed in other taxa.

- While the analyses in this thesis found no support for preferential origination of non-planktotrophic clades at high latitude, it was difficult to discount this hypothesis because there are relatively few Cretaceous spatangoid specimens from high palaeolatitudes. Future collections from Antarctica, southern South America and other regions that lay close to the poles in the Cretaceous would enable this question to be addressed with greater confidence. New collections, with more precise locality and sedimentological data recording, would also make it possible to answer questions about correlation between larval mode and geographical range, latitude and depth with greater confidence.

APPENDIX 1

WHAT IS THE PLESIOMORPHIC LARVAL MODE FOR THE POST-PALAEOZOIC ECHINOIDS?

INTRODUCTION

Sea urchins, like many marine invertebrates, employ two distinct strategies for development from a fertilized egg to an adult. The first of these strategies, planktotrophy, involves producing a large number of complex larvae that have the ability, and the need, to feed in the water column prior to settlement and metamorphosis. The alternative strategy, non-planktotrophy, involves the production of a smaller number of larvae that lack the complex structures required for feeding but are instead supplied with a large egg, which provides their nutritional requirements up to metamorphosis. Non-planktotrophy can be divided into two sub-categories: planktonic lecithotrophy, in which the larva lives in the water column until settlement and metamorphosis; and brooding, in which the larva is protected either among the spines or in a specialized brood pouch on the test of the female.

It has been widely assumed that planktotrophy is the plesiomorphic condition within the sea urchins. There are two major lines of evidence to support this assumption. Firstly, there are a large number of similarities between the feeding larvae of the different echinoderm classes; if non-planktotrophy were the plesiomorphic condition for echinoids then these similarities must have been acquired convergently (Strathmann 1978; Wray 1995; Smith 1997). Secondly, among sea urchins and other marine invertebrates, most clades of non-planktotrophs appear, by comparison with extant outgroups, to have evolved from planktotrophic ancestors (Strathmann 1978; Emlet 1991; Wray 1995; Jeffery *et al.* 2003; Sly *et al.* 2003). These phylogenetic arguments are further supported not only by the presence of structures interpreted as

vestigial feeding structures in the larvae of several non-planktotrophic echinoid species (Mortensen 1921; Amemiya & Emlet 1992; Olsen *et al.* 1993; Emlet 1995a), but also by the theoretical arguments that it is easier to lose complex feeding apparatus than to gain it, and that such losses may be irreversible (Strathmann 1978).

Understanding the ancestral larval mode in echinoids is important for evolutionary, developmental and genomic biologists, not least because it may have significant implications in terms of the broader relevance of developmental genetic data from the *Strongylocentrotus purpuratus* genome, which has recently been sequenced (Sea Urchin Genome Sequencing Consortium 2006). However, despite the widespread interest in the evolution of developmental mode within the echinoids, there has so far been no discussion of the phylogenetic distribution of larval strategies within the basal portions of the two major clades of post-Palaeozoic echinoids, the cidaroids and the euechinoids, which together contain all extant sea urchins. Furthermore, nothing has been published about the larval modes of Palaeozoic echinoids. Because the sea urchins passed through an extreme taxonomic bottleneck at the Permian-Triassic boundary it is not possible to extend inferences based on the larvae of extant echinoids to Palaeozoic taxa. Current thinking is that the cidaroids and euechinoids diverged prior to the Permian-Triassic boundary and that the ancestors of each group passed across the boundary and began to radiate from the Triassic onwards (Kier 1984). Examining the evolution of developmental strategy in the basal parts of these clades holds the key to determining the plesiomorphic condition for the post-Palaeozoic sea urchins. Here I explore this question by mapping data on larval modes in extant sea urchins (Emlet 1995b) onto phylogenies of the cidaroids (Smith & Wright 1989) and euechinoids (Smith *et al.* 2006).

MATERIAL AND METHODS

Cidaroids

I exploited the large dataset on the larval modes of regular echinoids, which was compiled by Emlet (1995b) but has not previously been considered within a phylogenetic framework. The data were mapped onto a phylogenetic tree of the cidaroids derived from the data matrix of Smith & Wright (1989). I believe that their analysis, which was based on a matrix of 28 morphological characters in 20 extant genera, is the most recent phylogenetic analysis of the cidaroids to have been produced. Because Smith and Wright (1989) did not describe the methodology used to produce the cladogram they present, their dataset was re-analysed here using parsimony within the computer programme PAUP* (Swofford 2002). All characters were assigned equal weight and were treated as unordered; multistate taxa were treated as polymorphisms.

The first step was to determine whether the dataset contained a significantly stronger phylogenetic signal than a random dataset. In order to test the null hypothesis that 'the dataset has no more phylogenetic signal than a random dataset' a permutation tail probability (PTP) test (100 replicates) was carried out on the dataset (see Faith & Cranston 1991). The null hypothesis would be rejected if the p-value were less than 0.05.

Trees were constructed using a branch and bound search because, although the dataset was too large for an exhaustive search, it was small enough that a branch and bound search could be used to find the most parsimonious trees (MPTs). The simple addition sequence offered within PAUP* was used. A strict consensus tree was used to summarise the information given in the MPTs.

The consistency index (CI) and retention index (RI) were both noted as measures of robustness. To produce an index of support, the bootstrap technique (Felsenstein 1985) was used (full heuristic search, 1000

replicates). The results were presented on the strict consensus tree. A decay analysis (Bremer support) (Bremer 1988, 1994) was carried out using the computer programme TREEROT (Sorensen 1996) in order to provide a measure of relative support for each clade. The decay index of a particular clade represents the number of additional steps required for a clade to be removed from the tree. The decay indices were also presented on the strict consensus tree.

Mapping larval strategy onto the resulting phylogeny enabled us to elucidate the plesiomorphic developmental mode for the cidaroids and resolve the number and direction of switches in developmental mode within the group.

Euechinoids

In order to understand the pattern of evolution of larval strategy in the euechinoids, data on larval modes from Emlet (1995b) were mapped onto the combined morphological and molecular tree for the Echinoidea as a whole presented by Smith *et al.* (2006). This tree is the semistrict consensus of six MPTs derived from parsimony analysis of the combined dataset presented by Smith *et al.* (2006). This enabled us to elucidate the number and direction of switches in the euechinoids.

RESULTS

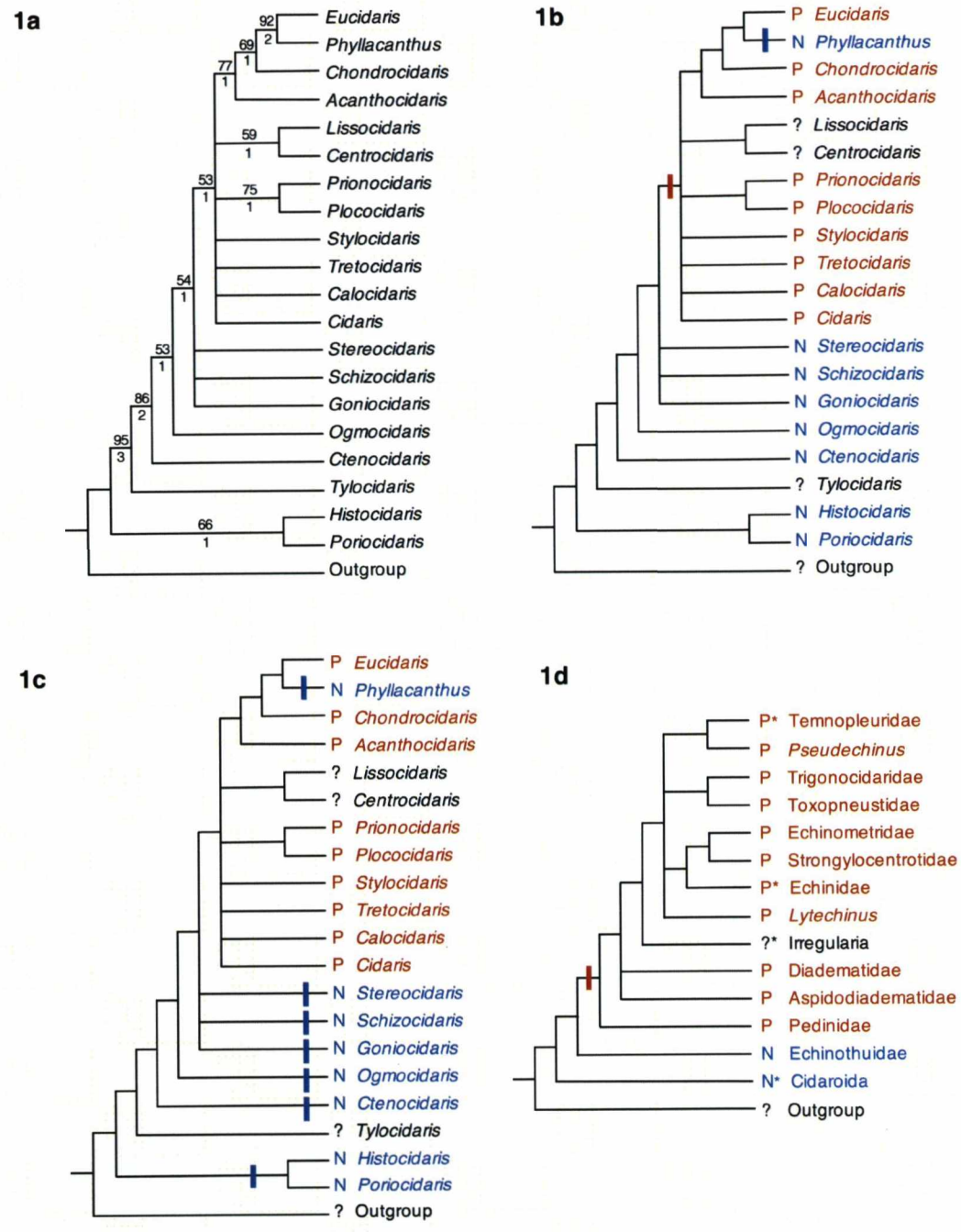
Cidaroids

The PTP test produced a p-value of 0.01 suggesting that the null hypothesis that the data has no more phylogenetic signal than random could be rejected. While Smith & Wright (1989) presented a single cladogram, my analysis of their data produced 40 MPTs of 55 steps (CI 0.727; RI 0.786), the strict consensus of which is presented in Figure 1a. Bootstrap support values are displayed above the branch leading to each node and decay indices are displayed below the branch. The topology of the strict

consensus tree differed slightly from Smith & Wright's (1989) cladogram, the most significant difference being that the goniocidarids, stereocidarids and ctenocidarids form a paraphyletic grouping in this analysis but are a monophyletic clade in Smith & Wright's cladogram.

The strict consensus tree with the most parsimonious arrangement of switches in developmental mode is shown in Figure 1b. The key finding of this analysis is that the most basal extant cidaroid family, the Histocidaridae (I use the taxonomic scheme of Smith 2005), has a non-planktotrophic larval strategy. I lack data on the next most basal group, the Psychocidarinae, which has only a single extant representative, *Tylocidaris ohshimai*. However, the Ctenocidarinae, which represent the next most basal group and the most basal clade within the family Cidaridae also employ non-planktotrophic larval strategies as do the next two subfamilies the Goniocidarinae and Stereocidarinae. Only the most derived cidaroid clade, the Cidarinae has planktotrophic development. Within the Cidarinae there is a reversal to non-planktotrophy in the genus *Phyllacanthus*. The most parsimonious explanation of this distribution of larval modes is that non-planktotrophy is plesiomorphic with planktotrophy evolving at the base of the Cidarinae (Figure 1b).

Figure 1.
Phylogenetic trees of echinoid taxa showing the distribution of planktotrophic (P, red) and non-planktotrophic (N, blue) larval strategies; switches from non-planktotrophy to planktotrophy are represented by red bars, switches from planktotrophy to non-planktotrophy are represented by blue bars. 1a. Strict consensus tree of cidaroid genera. The number above the branch leading to each node shows the bootstrap support value; the number below each node shows the decay index. 1b-c. Strict consensus tree of cidaroid genera with possible patterns of switches in larval mode. 1a shows the most parsimonious pattern of switches; 1b shows the most parsimonious distribution with only switches from planktotrophy to non-planktotrophy. 1d. Simplified version of the semistrict consensus tree of echinoid taxa produced by Smith et al. (2006) using parsimony analysis of combined morphological and molecular data. The most parsimonious distribution of switches in larval mode is shown. Asterisks represent taxa that include both planktotrophs and non-planktotrophs, the larval mode listed is the one that occurs in the most basal taxa based on available phylogenies (Cidaroida: this study; Echinometridae: Jeffery, unpublished data; Temnopleuridae: Jeffery et al. 2003).


1a
92
2
69
1
77
1
59
1
53
1
75
1
54
1
53
1
86
2
95
3
66
1
Eucidaris
Phyllacanthus
Chondrocidaris
Acanthocidaris
Lissocidaris
Centrocidaris
Prionocidaris
Plococidaris
Stylocidaris
Tretocidaris
Calocidaris
Cidaris
Stereocidaris
Schizocidaris
Goniocidaris
Ogmocidaris
Ctenocidaris
Tylocidaris
Histocidaris
Poriocidaris
Outgroup
1b
P Eucidaris
N Phyllacanthus
P Chondrocidaris
P Acanthocidaris
? Lissocidaris
? Centrocidaris
P Prionocidaris
P Plococidaris
P Stylocidaris
P Tretocidaris
P Calocidaris
P Cidaris
N Stereocidaris
N Schizocidaris
N Goniocidaris
N Ogmocidaris
N Ctenocidaris
? Tylocidaris
N Histocidaris
N Poriocidaris
? Outgroup
1c
P Eucidaris
N Phyllacanthus
P Chondrocidaris
P Acanthocidaris
? Lissocidaris
? Centrocidaris
P Prionocidaris
P Plococidaris
P Stylocidaris
P Tretocidaris
P Calocidaris
P Cidaris
N Stereocidaris
N Schizocidaris
N Goniocidaris
N Ogmocidaris
N Ctenocidaris
? Tylocidaris
N Histocidaris
N Poriocidaris
? Outgroup
1d
P* Temnopleuridae
P Pseudechinus
P Trigonocidaridae
P Toxopneustidae
P Echinometridae
P Strongylocentrotidae
P* Echinidae
P Lytechinus
?* Irregularia
P Diadematidae
P Aspidodiadematidae
P Pedinidae
N Echinothuidae
N* Cidaroida
? Outgroup

Euechinoids

The phylogeny of Smith *et al.* (2006) is shown in Figure 1d with data on larval modes mapped on to it. The key finding is that non-planktotrophy is the developmental strategy employed by all members of the echinothurids (the most basal clade of euechinoids) for which larval mode is known. As non-planktotrophy is also the larval strategy employed by the most basal members of the cidaroid clade, the most parsimonious explanation of the data is that planktotrophy was gained at the base of the acroechinoids (the clade containing all euechinoids apart from the echinothurids; Figure 1d). There were subsequently numerous transitions from planktotrophy to non-planktotrophy in derived positions within various euechinoid clades; these have been documented by a number of authors (e.g. Wray 1992, 1995; Smith *et al.* 1995a; Jeffery 1997; Jeffery & Emlet 2003; Jeffery *et al.* 2003).

DISCUSSION

Are the phylogenies correct?

When data on larval modes are mapped on to the phylogenetic trees presented in Figure 1 non-planktotrophic taxa are seen to lie in basal positions. However, one important possibility that must be considered is that the findings of this study are simply an artefact of using incorrect phylogenies, and that the true phylogenies would place planktotrophic taxa at the bases of the cidaroid and euechinoid clades.

The phylogenetic tree of cidaroids presented here is based on a parsimony analysis of morphological data. A molecular phylogeny would provide an independent test of cidaroid interrelationships but, to my knowledge, no such analysis has been produced to date. However, in the absence of such a test I feel that there is good evidence that the phylogeny is broadly correct, and

that it is highly unlikely that the principal finding that planktotrophy lies in a basal position is an artefact of incorrect phylogeny. Firstly, given the data presented in the matrix of Smith & Wright (1989), tree topologies in which the clade of planktotrophic taxa lies in a basal position are a minimum of 61 steps long. This is six steps longer than the original MPTs and represents an increase in tree length of more than 10%. Furthermore, a Templeton's test (Templeton 1983) reveals that many of these trees are a significantly less parsimonious explanation of the data than the original MPTs. In addition, the branching order of cidaroid higher taxa in the tree is largely consistent with their first appearances in the fossil record: the only part of the tree where there is disagreement concerns the ctenocidarids which appear in the fossil record later than the stereocidarids and goniocidarids. Thirdly, the phylogenetic relationships are in broad agreement with traditional schemes of cidaroid phylogeny (e.g. Mortensen 1928; Durham & Melville 1957; Phillip 1963, 1964; Fell 1966).

I are also confident that the tree for euechinoids is broadly correct because the same relationships are derived from maximum likelihood analysis of molecular data (figure 2 of Smith *et al.* 2006), as well as parsimony analysis of both morphological data (figure 2 of Smith *et al.* 2006) and combined morphological and molecular data (figure 3a of Smith *et al.* 2006) (though, intriguingly, Bayesian analysis of the combined dataset (figure 3b of Smith *et al.* 2006) gives a different topology with echinothurids in a more derived position; it should also be noted that this is one of the few portions of the echinoid tree where there is disagreement between the fossil record and molecular clock (Smith *et al.* 2006)). A basal position for the echinothurids within euechinoids is widely accepted (Mooi *et al.* 2004) and is supported by previous phylogenetic analyses (Jensen 1981; Smith 1984; Littlewood & Smith 1995).

Plesiomorphic non-planktotrophy or parallel acquisitions of non-planktotrophy?

Two possible scenarios

The most parsimonious explanation of the data presented here is that non-planktotrophy is the plesiomorphic condition for the post-Palaeozoic echinoids and that the planktotrophic strategy evolved twice: once within the cidaroid clade (at the base of the Cidarinae; see Figure 1b) and once within the euechinoid clade (at the base of the Acroechinoidea; see Figure 1d).

An alternative, but less parsimonious, explanation is that planktotrophy is the plesiomorphic condition for post-Palaeozoic sea urchins and that non-planktotrophy evolved in the stem groups of each of the non-planktotrophic clades that lie at the base of the cidaroids (Figure 1c) and the euechinoids. Given the phylogenies presented here this would require multiple shifts: at least five in cidaroids and one in euechinoids. (It should be noted that if the goniocidarids, stereocidarids and ctenocidarids in fact form a monophyletic grouping – as suggested by Smith & Wright (1989) but not supported by this analysis – then this would reduce the number of additional switches required, but plesiomorphic planktotrophy would remain the most parsimonious explanation.)

If future developmental or palaeontological studies (see below) show this second scenario to be correct, then this also requires explanation. Why should it be that the most basal clades of cidaroids and euechinoids, and also ophiuroids (Smith 1997), all lost planktotrophy independently? One possible explanation is that, because switches from planktotrophy to non-planktotrophy are considered to be more likely than switches in the opposite direction and possibly irreversible (Strathmann 1978), it is anticipated that the proportion of non-planktotrophs in a clade will increase through time (Hansen 1978, 1983; Duda & Palumbi 1999; Hart 2000). Eventually this

might result in older clades containing solely non-planktotrophic taxa. In addition, it is possible that planktotrophic taxa are more susceptible to mass extinction events (Valentine & Jablonski 1986, but see also Smith & Jeffery 1998). However, these factors must be balanced against the fact that background extinction rates are lower in planktotrophic taxa (though speciation rates are also lower) (Hansen 1978, 1980, 1982, 1983; Jablonski & Lutz 1983; Jablonski 1986; Jeffery & Emlet 2003). While the interplay between these factors remains poorly understood, they represent a possible explanation for the predominance of non-planktotrophic taxa in basal positions within major clades.

Because a scenario with plesiomorphic planktotrophy involves additional switches in larval mode it is less phylogenetically parsimonious. However, given the likelihood that complex planktotrophic larvae are more easily lost than reinvented (Strathmann 1978), a case could be made that parallel acquisition of non-planktotrophy in each of the basal clades is actually the more likely scenario. Such arguments have been made in other taxonomic groups. For example, most malacostracan crustaceans have a reduced 'egg nauplius' larva but two taxa, the euphausiids and dendrobranchiates, have a complex locomotory 'free nauplius' larva, which is also found in the lineage leading to the malacostracans. The most parsimonious explanation involves the complex free nauplius evolving once or, at most, twice from taxa with egg nauplii within the malacostracans. Scholtz (2000) considers this explanation to be the more likely citing independent evidence from the homology of larval characters. On the other hand, D. Waloszek (personal communication to Strathmann & Eernisse 1994) has suggested that the multiple appearance of egg nauplii (between five and eight times) is more plausible than the 'resurrection' of the complex free nauplius. Hart *et al.* (1997) discuss a similar example in asterinid starfish. Here the most parsimonious explanation of the data requires switches from non-planktotrophy to planktotrophy, but Hart *et al.* (1997) argue that similarities in

larval form and the lack of "obvious homoplasies" suggest that parallel acquisition of feeding larvae probably did not occur. Similarly, Smith (1997) notes that all deep branches of the ophiuroid cladogram presented by Smith *et al.* (1995b) have only non-planktotrophic development and only one major derived clade (Ophiurina) has planktotrophic larvae. However, Smith (1997) considered it inherently unlikely that ophiuroids are really non-planktotrophic primitively because of the convergence required.

At present there is no objective method for deciding which of the two alternatives described above is the more likely. In the following sections I discuss the arguments for and against each explanation and suggest future research that may enable us to definitively distinguish the two possibilities.

The likelihood of gain and loss of feeding larvae

One suggestion is that the likelihood of gain and the likelihood of loss of a trait may not be the same and so assuming equal likelihood in analyses is flawed (Omland 1997; Cunningham *et al.* 1998; Keever & Hart 2008). However, because there is currently no way of quantifying how much more likely the loss of planktotrophy may be in comparison to its gain, I do not take this approach.

One factor that may make the plesiomorphic status of planktotrophy seem less likely is the amount of convergent evolution it implies. The finding that several of the most basal echinoid clades exhibit non-planktotrophic development suggests that the most parsimonious explanation is that the pluteus larvae of echinoids evolved independently from the feeding larvae of the other echinoderm classes (Figure 1b) and that any similarities represent convergent evolution. Furthermore, as the most basal euechinoids are also non-planktotrotrophs, the most parsimonious explanation of the data presented here is that planktotrophy evolved independently in cidaroids and euechinoids (Figure 1d), which requires that the plutei of these two clades

also evolved convergently. Previous workers have considered both of these scenarios to be unlikely in the extreme. For example Strathmann (1978) argued that the larvae of echinoids, holothuroids, crinoids, asteroids and ophiuroids were "so similar in structure and development that descent from an ancestor with a planktotrophic larva is indicated", and Wray & Raff (1991) wrote that: "the probability that the plutei of different [echinoid] orders are convergent is vanishingly small given the high degree of similarity in their complex morphology."

Using data from *Eucidaris thouarsi* – the only planktotrophic cidaroid to have had its development up to metamorphosis studied in detail (Emlet 1988) – and from other planktotrophic echinoderms, Wray (1992) provided a list of characters shared by echinoderm feeding larvae (table 2a of Wray 1992), and echinoid plutei (table 2b-d of Wray 1992), which argue for a single origin of the echinoderm feeding larva. In particular, he pointed out that the plutei of Cidaroidea and Euechinoidea share the following characters which he considered to have been present in the larva of the crown group echinoid ancestor: (1) the full complement of six skeletal elements found in extant echinoplutei; (2) eight or ten arms (paired postorals, posterodorsals, preorals, anterolaterals, and perhaps posterolaterals); (3) fenestrated postoral and posterodorsal arm rods; and (4) dorsal, ventral, and posterolateral vibratile lobes.

However, there are also important differences between the feeding larvae of the different echinoderm classes and, what is more, the phylogenetic relationships of the classes require considerable convergent evolution (e.g. Strathmann & Eernisse 1994). For example, phylogeny (Strathmann & Eernisse 1994), dissimilarities in the morphology of the larval apical organs (Byrne *et al.* 2007), and numerous differences in development (Primus 2005) all suggest the similarities between the pluteus larvae of echinoids and ophiuroids represent convergence (Byrne *et al.* 2007). There are also

important differences between the plutei of cidaroids and euechinoids. Emlet (1988) highlighted a number of important differences between the larvae of *Eucidaris thouarsi* and those of euechinoids, the most notable being the absence of the vestibule in *E. thouarsi* (see table 2 of Emlet 1988 for a comprehensive list).

The independent evolution of the long list of characters shared by the feeding larvae of cidaroids, euechinoids, and other echinoderms would represent a remarkable example of convergence. However, in principle, gaining planktotrophy is relatively simple to evolve, as it requires only an animal with sufficient mass to produce the large number of eggs required for planktotrophy (Olive 1985; Chaffee & Lindberg 1986) and a relatively trivial shift in the timing of development of the gut (Peterson 2005). Furthermore, convergent evolution has been demonstrated to be prevalent in biology in general (Conway Morris 2003), and in larvae in particular (e.g. Reid 1989; Wray 1996; Hart 2000; Rouse 2000; Peterson 2005), with Smith *et al.* (1995a) showing empirically that larval characters are more homoplastic than adult characters in sea urchins. The role of functional requirements may be particularly strong in determining the morphology of larvae (e.g. Emlet 1991, Conway Morris 1998; Strathmann 2000).

It is also worth noting here that hypotheses of convergent evolution of larval forms, previously considered highly unlikely, are rapidly gaining widespread support in other portions of the tree of life. Peterson *et al.* (1997), for example, dismissed the notion that the similar larvae of distinct sets of phyla could be due to 'parallel evolution' as "the epitome of hand waving." A decade on, however, it has been convincingly argued that the trochophore larva (*sensu* Nielsen 1995) has been derived independently four times (in Echiura, Entoprocta, Polygordidae and Serpulidae; Rouse 2000) and that downstream larval feeding has been independently gained at least 11 times (Rouse 2000). What is more, several authors have proposed, based on

phylogenetic and theoretical grounds, that the last common ancestor of the Bilateria lacked feeding larvae and that planktotrophy evolved convergently in several different phyla (e.g. Haszprunar *et al.* 1995; Conway Morris 1998; Wolpert 1999; Jenner 2000; Rouse 2000; Sly *et al.* 2003; Peterson 2005, Raff 2008).

In summary, there are a large number of important similarities between the feeding larvae of echinoids and other echinoderm classes and between those of cidaroids and euechinoids; these suggest a single origin for the echinoderm feeding larva. On the other hand, there are also important differences between these larvae. In addition, convergent evolution is known to be prevalent in biology in general and in larval biology in particular. At present there is no objective method to determine whether convergent evolution of similar feeding larval forms is more or less likely than multiple switches to non-feeding larvae. We must instead turn our attention to other data that may help to resolve this issue.

Evidence from extant larvae

Studies of extant echinoid larvae should provide data key to addressing the question of which larval strategy is plesiomorphic for the clade. Surprisingly, however, few of the pertinent taxa have had their development documented in detail. For example, much of our knowledge of cidaroid development comes from *Eucidaris thouarsi*, the only planktotrophic cidaroid to have had its development up to metamorphosis described comprehensively (Emlet 1988; see discussion above). The only other cidaroids for which detailed developmental information is available are *Phyllacanthus imperialis* and *P. parvispinus* (Olsen *et al.* 1993; Parks *et al.* 1989), which are shown by this analysis to have secondarily lost feeding larvae. No detailed information is available on the larvae of the basal cidaroids with non-planktotrophic development.

A single echinothurid, *Asthenosoma ijimae*, has had its development carefully described by Amemiya & Emlet (1992). It is uniformly ciliated rather than having a ciliated band and exhibits a reduced pluteus skeleton and an archenteron that is invaginated two-thirds of the way into the blastocoel (intermediate between pluteus larvae and previously described non-planktotrophic larvae). These features strongly suggest that *A. ijimae* is descended from ancestors with planktotrophic development. (But see Marshall *et al.* 1994, McEdward & Janies 1997, Janies 2003 and Collin *et al.* 2007 for discussion of the possibility of reversibility of losses of larval feeding.)

Study of the larval development of the non-planktotrophic taxa at the base of the cidaroid clade also has the potential to yield important information about the evolution of development within the cidaroids. For example, the complete absence of vestigial feeding structures within these taxa would suggest that non-planktotrophy was plesiomorphic for the cidaroids. Alternatively, the presence of larvae with reduced feeding structures would suggest that planktotrophy is primitive and that feeding larvae have been lost repeatedly in these groups.

Inferring the larval strategies of fossil taxa

The fact that both cidaroids and euechinoids have long stem groups of extinct taxa means that inferences based on extant taxa may become tenuous, so it is highly desirable to have direct data on these extinct stem group forms to bring to bear on the issue. The fossil record is the only direct source of data on the development of extinct organisms and such data, when considered in a phylogenetic context, has the potential to allow us to reconstruct the distribution of larval modes of stem group taxa. Thus, one line of future research that may prove fruitful is to use the crystallographic method described by Emlet (1985, 1989). This makes it possible to use the crystallographic orientations of the apical disc plates in fossilized adult

specimens to determine the larval strategies of extinct taxa at the base of the echinoid clade. This technique could be applied both to extinct cidaroid and echinothuroid taxa as well as to Palaeozoic and early Mesozoic stem group taxa in order to gain a better understanding of the plesiomorphic condition for the post-Palaeozoic echinoids.

What drives switches to planktotrophic development?

If non-planktotrophy is the plesiomorphic condition for post-Palaeozoic echinoids then one implication is that switches between planktotrophy and non-planktotrophy must have occurred in both directions in the geological past. This would indicate that, at least at some times in geological history, producing large numbers of widely dispersing feeding larvae has been actively selected for. Peterson (2005) has argued, on the basis of phylogenetic and molecular clock data, that this is the case around the Cambrian-Ordovician boundary when planktotrophy evolved independently in at least four (and perhaps as many as eight) clades. Peterson's (2005) study should serve to remind us of the dangers of applying the uniformitarian principle too rigorously: the fact that shifts from planktotrophy to non-planktotrophy have been common in the recent geological past does not necessarily mean that this has been the case throughout geological history. The study is also in agreement with the suggestion of Jeffery (1997) that extrinsic factors operating at particular times may drive co-ordinated shifts in developmental strategy.

Peterson (2005) suggested that, in the case of the shifts at the Cambrian-Ordovician boundary, the driving factor was the radiation of benthic suspension feeders with planktotrophy evolving in order to swamp these predators with numbers. However, it is not clear what factors could have driven shifts to planktotrophy some time after the divergence of the Cidarinae from the remaining cidaroids. One possibility is that the taxa that passed through the taxonomic bottleneck at the Permian-Triassic boundary

did so because they were non-planktotrophic. Planktotrophs seem to have been selected against during this mass extinction (Valentine & Jablonski 1986), although this does not appear to be the case in prosobranch gastropods or echinoids at the Cretaceous-Tertiary boundary (Valentine & Jablonski 1986; Smith & Jeffery 1998). Planktotrophy could then have evolved in the aftermath of the mass extinction to exploit either a general advantage of this developmental strategy, or an advantage specific to the early Mesozoic.

CONCLUDING REMARKS

I have demonstrated that the most basal extant members of the two major post-Palaeozoic echinoid clades employ non-planktotrophic larval strategies. The most phylogenetically parsimonious explanation of this data is that non-planktotrophy was the plesiomorphic condition for the post-Palaeozoic sea urchins. If this is indeed the case, then the planktotrophic pluteus larvae of cidaroids and euechinoids must be independently derived from non-planktotrophic ancestors and, furthermore, both must have evolved independently from the feeding larvae of the other echinoderm classes.

As well as calling into question the widely held assumption that planktotrophy is plesiomorphic for the post-Palaeozoic echinoids, the unexpected results of this study emphasise the importance of considering developmental data in a phylogenetic framework. In particular, the phylogenetic perspective reveals key gaps in our knowledge of echinoid larval development and highlights potentially fruitful areas for future research. For example, study of the development of the non-planktotrophic taxa at the base of the cidaroid clade would fill an important gap in our knowledge of echinoid development and could provide vital data to help us understand the evolution of echinoid development. I hope that future workers fully consider the phylogenetic framework when discussing larval

evolution and the homology of larval characters when choosing taxa in which to study development.

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Appendix 2: Larval modes inferred by crystallographic analysis. Specimens denoted [1] were analysed by Jeffery (1997), those denoted [2] were analysed by R. B. Emlet (unpublished data); all other specimens were analysed as part of this thesis. AMNH = American Museum of Natural History; MNHN = Museum National d'Histoire Naturelle, Paris; NHM = The Natural History Museum, London; NHMW = Natural History Museum, Vienna; USNM = Smithsonian Institute, Washington DC; UGHM = Hunterian Museum, Glasgow.

Taxon	Specimen No.	Larval Mode	Age	Location
Aphelaster integer	MNHN L21202	Planktotrophic	Neocomian	France
Bolbaster bexari	NHM E32070	Planktotrophic	Albian	Texas
Bolbaster cranium	USNM PAL 467474	Planktotrophic	U Albian/L Cen	Texas
Bolbaster gauthieri	NHM (Smith Coll.)[2]	Planktotrophic	?	?
Bolbaster paronai	NHM EE5034[1]	Planktotrophic	Maastrichtian	UAE
Bolbaster prunella	MNHN L22354	?	"Aturian"	France
Bolbaster prunella	NHM E4381[1]	Planktotrophic	"Dordonian"	France
Bolbaster punctatus	NHM E10384	Planktotrophic	Senonian	France
Coraster beneharnicus	NHM EE4825[1]	Planktotrophic	(Danian)	Spain
Coraster beneharnicus	NHM E8389	Planktotrophic	Maastrichtian	Spain
Cottreaucorys blayaci	NHM EE8132	Planktotrophic	Maastrichtian	Spain
Cyclaster integer	MNHN R68014	Planktotrophic	(Danian)	France
Cyclaster integer	NHM EE5585[1]	Non-planktotrophic	(Early Danian)	Kazakhstan
Cyclaster pfenderae	MNHN R68015	?	Upper Campanian	Madagascar
Cyclaster vilanovae	NHM EE ?[1]	Non-planktotrophic	(Danian)	Spain
Diplodetus americanus	AMNH 76285[1]	Non-planktotrophic	Camp-Maas	USA
Diplodetus americanus	USNM PAL 467181	? Too delicate	Cretaceous	Mississippi
Epiaster blanckenhorni	NHM EE1961	?	?	UAE

Epiaster dartoni	USNM PAL 467480	Planktotrophic	Aptian	New Mexico
Epiaster meridanensis	MNHN L21268	Planktotrophic	Turonian	France
Epiaster meridanensis	NHM E4979	?	Turonian	France
Gibbaster brevis	MNHN L23036	?	Santonian	France
Gibbaster gibbus	NHM E35551	Planktotrophic	Campanian	England
Gregoryaster jacobi	MNHN R67915	Planktotrophic	Maastrichtian	Madagascar
Hemiaster bosei	NHM E76539	?	Upper Turonian	Texas
Hemiaster brossardi	MNHN L22097	Planktotrophic	Campanian	Algeria
Hemiaster hattaensis	NHM EE4055[1]	Planktotrophic	Late Camp/Maas	UAE
Hemiaster wetherbyi	USNM PAL 467998	?	Maastrichtian	Mississippi
Heteraster bravoensis	NHM E81494	Planktotrophic?	Late Albian	Texas
Heteraster mexicanus	USNM PAL 467415	Planktotrophic	Middle Albian	Texas
Heteraster riovistae	USNM PAL 467273	Planktotrophic	Upper Albian	Texas
Heteraster riovistae	USNM ?[2]	Planktotrophic	Lower Cretaceous	Texas
Heteraster syriacus	NHM EE4631	?	Aptian	UAE
Heteraster syriacus	NHM EE4632	?	Aptian	UAE
Heteraster texanus	NHM EE4641	Planktotrophic	Albian	Texas
Heterolampas maresi	MNHN R67747	Non-planktotrophic	Campanian	Algeria
Holanthus hawkinsi	NHM E20098[1]	Planktotrophic	(Danian)	Madagascar
Holcopneustes cristatus	MNHN L22536	Planktotrophic	Senonian	Madagascar
Homoeaster auberti	MNHN L22622	Planktotrophic	Senonian	Tunisia
Homoeaster tunetanus	MNHN L22611	?	?	Tunisia
Homoeaster tunetanus	NHM EE4404[1]	Planktotrophic	(Danian)	Spain
Homoeaster tunetanus	MNHN L22617	Planktotrophic	Maastrichtian	Tunisia
Homoeaster tunetanus	NHM EE8397	Planktotrophic	Maastrichtian	Spain

Homoeaster tunetanus	NHM EE2372	?	Maastrichtian?	Mozambique
Iraniaster affinidouvillei	USNM PAL 464701	Planktotrophic?	Campanian	Saudi Arabia
Iraniaster affinidouvillei	NHM E79718	Planktotrophic	Campanian	Oman
Iraniaster bowersi	USNM PAL 464704	?	Late U Cretaceous	Saudi Arabia
Iraniaster douvillei	UGHM E325[1]	Planktotrophic	Camp-Maas	Somalia
Iraniaster douvillei	NHM E40574[1]	Planktotrophic	Camp-Maas	Iran
Iraniaster douvillei	MNHN L20848	?	Senonian	Iran
Iraniaster morgani	MNHN L20849	Planktotrophic	Senonian	Iran
Isaster acquitanicus	NHM EE4524[1]	Planktotrophic	Maas/Palaeocene	Spain
Isaster acquitanicus	MNHN L21304	?	Senonian	France
Leiostomaster bigoneti	NHM E79415	Non-planktotrophic	Campanian	Angola
Leiostomaster verrucosus	MNHN R67756	?	Santonian	Algeria
Leymeriaster leymerieri	NHM E45372	?	Turonian	France
Leymeriaster leymerieri	NHM (Smith Coll.)[2]	Planktotrophic	Maastrichtian	France
Leymeriaster nucleus	MNHN L22332	Planktotrophic	Turonian	?
Leymeriaster similis	NHM (Smith Coll.)[2]	Planktotrophic	Cenomanian	France
Leymeriaster simlis	MNHN L22432	Planktotrophic	Cenomanian	France
Leymeriaster subsimilis	NHM EE2321	Planktotrophic	Cenomanian/Turonian	India
Linthia payeni	MNHN L22870	Planktotrophic	Campanian	Algeria
Linthia sudanensis	MNHN R67875	Planktotrophic?	(Eocene)	Mali
Linthia sudanensis	NHM EE2262[1]	Planktotrophic	(Thanetian)	Niger
Macraster sp.	NHM EE4610	Planktotrophic?	Late Albian	Texas
Macraster vatonnei	MNHN R67559	Planktotrophic	Cenomanian	Tunisia
Macraster whitei	USNM PAL 466854	Planktotrophic	Middle Albian	Texas
Mauritanaster mirabilis	NHM E4052[1]	Non-planktotrophic	Senonian	Algeria

Mauritanaster mirabilis	MNHN L22318	Non-planktotrophic	"Dordonian"	Algeria
Mecaster aumalensis	MNHN R67653	Planktotrophic?	Cenomanian	Algeria
Mecaster batnensis	NHM EE191	Planktotrophic	Cenomanian	Tunisia
Mecaster batnensis	USNM PAL 468563	Planktotrophic	Cenomanian	New Mexico
Mecaster charmesi	MNHN L22900	Planktotrophic?	Santonian	Tunisia/Algeria border
Mecaster durandi	MNHN L22902	?	Santonian	Algeria
Mecaster fischeri	MNHN L22907	Planktotrophic	Cenomanian	Algeria
Mecaster fourneli	USNM PAL 468896	Planktotrophic	Coniacian	Algeria
Mecaster fourtaui	NHM EE2353	Planktotrophic?	Cenomanian	India
Mecaster fourtaui	NHM E4034[1]	Planktotrophic	Cenomanian	Algeria
Mecaster heberti	MNHN L22908	Planktotrophic	Cenomanian	Algeria
Mecaster heinzi	MNHN L22909	?	Turonian	Algeria
Mecaster inconstans	MNHN L22910	Planktotrophic	Maastrichtian	Madagascar
Mecaster messai	USNM PAL 468942	Planktotrophic	Santonian	Algeria
Mecaster nicaisei	MNHN L22329	Planktotrophic	Cenomanian	Tunisia
Mecaster oblongus	MNHN L22913	Planktotrophic	Turonian	Algeria
Mecaster orbignyi	MNHN R68001	Planktotrophic	Cenomanian	Algeria
Mecaster sp.	NHM EE2432	Planktotrophic	Cenomanian	Tunisia
Mecaster texanum	USNM PAL 468921	Planktotrophic	Upper Cretaceous	Texas
Mecaster thalensis	MNHN L22915	Planktotrophic	Turonian	Algeria
Mecaster verneuili	NHM E4176	Planktotrophic?	Turonian	France
Mecaster verneuili	MNHN L22922	Planktotrophic	Turonian	Algeria
Mecaster victoris	NHM EE4048	?	Maastrichtian	UAE
Micraster beonensis	MNHN L23015	Planktotrophic	Upper Turonian	France
Micraster caretonensis	MNHN L23054	? Too delicate	Coniacian	Spain
Micraster decipiens	MNHN L23208	Planktotrophic	?	France
Micraster leskei	MNHN L23280	Planktotrophic	Turonian	France
Micraster leskei	NHM E9892	Planktotrophic	Turonian	?
Micraster normanniae	MNHN L23348	Planktotrophic	Upper Turonian	France
Micraster nutrix	MNHN L23359	?	Maastrichtian	Madagascar
Micraster santaemurae	MNHN L23374	?	Turonian	France
Micraster schroederi	NHM E75821	Planktotrophic	Mid Lower Campanian	Germany
Micraster turonensis	MNHN L23417	?	Coniacian	France
Micraster turonensis	NHM E40974	?	Senonian	France
Mokotibaster hourcqi	NHM E79094	Planktotrophic	Lower Maastrichtian	Madagascar
Opissaster somaliensis	NHM E582[1]	Planktotrophic	(Palaeocene)	Somalia
Orthaster dagestanensis	NHMW 2005z0083/0125	Planktotrophic	(Danian)	Austria
Ovulaster auberti	MNHN L23437	?	Maastrichtian	Algeria
Ovulaster auberti	MNHN L23439	Planktotrophic?	Maastrichtian	Tunisia
Ovulaster truncatus	MNHN L23442	?	Maastrichtian	Algeri
Palhemiaster calvini	USNM PAL 467446	Planktotrophic	Lower Cenomanian	Texas
Palhemiaster peroni	MNHN L22592	Planktotrophic	Aptian	Algeria
Paraster variabilis	USNM PAL 465385	Planktotrophic	Maastrichtian	Mississippi
Periaster elatus	MNHN L22903	Planktotrophic?	Cenomanian	France
Plesiaster nobilis	NHM E82582	?	U. Camp/L. Maas	Oman
Plesiaster peini	MNHN L23362	?	Santonian	Algeria

Plesiaster peini	NHM EE7698	Planktotrophic	Lower Campanian	Tunisia
Pliotoxaster ?lyonsi	NHM E9392	Planktotrophic	Upper Cretaceous	Lebanon
Pliotoxaster dieneri	NHM E73207	?	Albian	Lebanon
Pliotoxaster sp. nov.	MNHN L21200	Planktotrophic?	Cenomanian	Spain
Proraster geayi	MNHN L22940	?	Maastrichtian	Madagascar
Proraster morgani	MNHN L22941	Planktotrophic	?	Iran
Toxaster africanus	MNHN L21004	?	Neocomian	Algeria
Toxaster amplus	MNHN L21010	?	Hauterivian	France
Toxaster collegnoi	MNHN L21041	?	Aptian	Algeria
Toxaster collegnoi	MNHN L21036	?	Aptian	France
Toxaster complanatus	NHM E43810	Planktotrophic	Neocomian	France
Toxaster lorioli	MNHN L21071	Planktotrophic?	Neocomian	France
Toxaster oblongus	NHM 56422	?	Aptian	Switzerland
Toxaster retusus	NHM E83246	Planktotrophic	Hauterivian	France
Toxaster retusus	MNHN L21107	?	Neocomian	France
Toxaster ricordeaui	MNHN L21140	?	Neocomian	France